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REVISION OF THE CRANE FLY GENUS DICRANOPTYCHA IN NORTH AMERICA[1]

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Abstract

Twenty-three nearctic species are recognized. *D. microphallus* is a synonym of *septemtrionis* and *D. rogersi* a synonym of *sobrina*. *D. byersi* (Appalachian North Carolina and Tennessee) and *D. spinifera* (Appalachian Mountains from Pennsylvania to northern Georgia) are described as new. External morphology of adults, larvae and pupae, ecological occurrence, life cycle and behavior are discussed. All species are described uniformly, illustrated, and identified by a key. Geographic and seasonal distributions of each are summarized. Phylogenetic relationships of *Dicranoptycha* to other Limoniinae are considered, and geographic distribution of nearctic species groups is interpreted in comparison to worldwide distribution of the genus.

Introduction

Although the subfamily Limoniinae includes many genera with large numbers of nearctic species, only one comprehensive generic revision, on *Chionea* (Byers, 1983), has been undertaken for the entire region. For the family Tipulidae as a whole, the only other monographic revision of a major genus so far published in North America is that on *Dolichopeza* (Byers, 1961).

One limoniine genus in which the taxonomy has been complicated due to a lack of a sound morphological basis is *Dicranoptycha* Osten Sacken, which at present includes 23 nearctic species (Alexander, 1965:52). A revision of the five European species of this genus was published by Starý (1972). Alexander (1942, 1967) dealt with ten eastern and six western Nearctic species.

Difficulties were encountered with the existing keys in identifying some *Dicranoptycha* species from eastern Kansas. These keys rely heavily on color characters and do not include females. Original descriptions were often inadequate due to a lack of specific characters, lack of figures of distinctive structures, incorrect illustrations, and inconsistent usage of anatomical terms which were not in agreement with the current understanding of morphology of Tipulidae. After examining the type specimens, it became obvious that many specimens in collections were misidentified.

The primary object of this revision is to present a taxonomic treatment of *Dicranoptycha* of North America. Attempts have been made to define species using morphological characters, especially of male and female genitalia, and less emphasis has

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been placed on color. Illustrations and keys based on morphological characters of both male and female are provided to assist in the identification of species. A second object is to examine series of specimens from various localities and study the variation to determine what constitutes a species within this genus. Since so little biology of crane flies has been studied and since many regional faunas are still incompletely known, the zoogeography and phylogeny of *Dicranoptycha* as presented here are tentative.

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I thank Dr. George W. Byers, who introduced me to the study of crane flies, for his advice on many occasions, for his willingness to help at any time, for his patience in improving the manuscript, and above all for his concern during my stay in the United States. This study was supported by the National Science Foundation under Grant DEB-77-15868, George W. Byers principal investigator.

A most pleasant and profitable visit was to Amherst, Massachusetts, as the guest of the late Dr. Charles P. Alexander, who took time to show me his personal collection of Tipulidae in "Crane Fly Haven" and allowed me to examine the types and other specimens of *Dicranoptycha*. I also thank the faculty and students of the Department of Entomology, University of Kansas, for their support and helpful discussions, particularly Dr. Charles D. Michener and Dr. Peter D. Ashlock, who read and criticized this paper.

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MATERIALS AND METHODS

Nearly 3500 specimens have been examined for this study. Most were collected from their natural habitats, and are preserved in the Snow Entomological Museum, University of Kansas (SEM), but many were borrowed from other entomological collections. Besides intensive field collecting carried on in the principal study area, the oak-hickory forest of eastern Kansas, field collections were made in other regions of the United States, including the Appalachian Mountains, the Sierra Nevada, and other parts of California.

Institutions loaning material used in this study (and abbreviations used below) are the following: American Museum of Natural History (AMNH), California Academy of Sciences (CAS), Canadian National Collection (Department of Agriculture) (CNC), Cornell University (CU), Florida State Collection of Arthropods (FSCA), Harvard University (MCZ), Los Angeles County Museum of Natural History (LACM), National Museum of Natural History (NMNH), University of California (Berkeley, Davis, and Riverside) (CIS, UCD, UCR), University of Michigan Museum of Zoology (UMMZ), and Washington State University (WSU).

Type specimens of most of the North American and several exotic species of *Dicranoptycha* have been examined in the collection of Charles P. Alexander at Amherst, Massachusetts, which is now housed in the NMNH.

Net sweeping was the basic method of collecting. Inspections were made at potential habitats, places where the forest has poorly developed understory trees, and where the forest floor is generally open and dominated by short undergrowth (45 - 60 cm), partially shaded, with humidity low enough that grass is usually absent. In such habitats, flies were taken either at their resting sites, or in the air as they took flight. Specimens were either mounted or preserved in 70% alcohol. Most mating pairs were preserved in alcohol. The methods used for preparation of field collected material are those of Byers (1961: 677).

External structural characteristics of adults were examined on pinned specimens and on specimens preserved in alcohol when possible. Male and female genitalia for dissection were prepared by removing the posterior abdominal segments and gently boiling them in a solution of 10% KOH for about three minutes to soften the structures enough to be easily dissected. They were rinsed with acetic acid and water after removal from KOH before being placed in glycerine for examination. Dissected parts were preserved in glycerine in a microvial attached to the appropriate specimen pin. Line drawings of internal reproductive structures were made from these KOH-treated specimens. Only two measurements of adult *Dicranoptycha* were made, body length and wing length. The former is the straight-line distance from the anterior end of the head to the tip of the abdomen; the latter is

the straight-line distance between the attachment of the wing and its tip. All measurements were made with the aid of an ocular grid.

Larvae were collected at the University of Kansas Natural History Reservation, about 5 miles northeast of Lawrence, Kansas. Field collected larvae provided with organic debris from the natural habitat grew in the laboratory and transformed into pupae and adults normally. Attempts to rear larvae from eggs were unsuccessful. Adult females usually are unwilling to oviposit in the laboratory; however, if the mature adult female is pinched at the neck region with a pair of fine forceps, she will start ovipositing and usually finish laying all the eggs in a short period. Methods for preserving larvae and pupae are those of Byers (1961: 679).

Field observations of *Dicranoptycha* species in their natural habitats were made at numerous places in addition to the principal study area. These included data about their natural history, behavior, and ecology.

The Genus *Dicranoptycha* Osten Sacken

The genus *Dicranoptycha* was first proposed in 1859 by Osten Sacken. His four included species were *Dicranoptycha germana, nigripes, sobrina,* and *sororcula.* In 1869, Osten Sacken redescribed the genus and recognized *D. sororcula* as a synonym of *sobrina.* Since Osten Sacken did not mention a type species, *D. germana* was subsequently so designated by Coquillett (1910). About 80 species have been recognized from most of the major land masses. There is one fossil record from the Baltic Amber. Until recently, the genus has not been divided into subgenera. In 1970 Savchenko placed a single species, *D. mirabilis,* from Soviet Central Asia (Tajikistan, Turkmenistan), in a separate subgenus *Ulugbekia,* on the basis of its hypopygial structures.

Twenty-three North American species are recorded by Alexander (1965). Of these, I regard 21 as valid. *D. microphallus* and *rogersi* are treated in this study as synonyms of *septemtrionis* and *sobrina,* respectively. Two new species, *D. byersi* and *spinifera,* are described below.

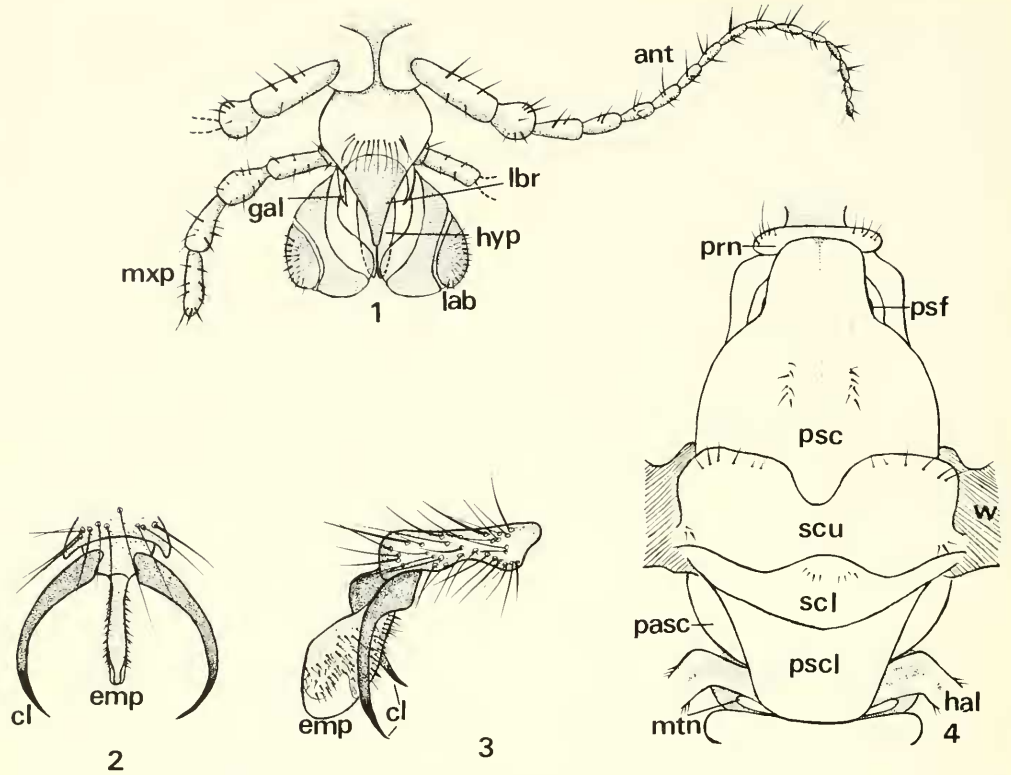
External Morphology of Adults

This section is presented to clarify terminology used as a basis for the following taxonomic descriptions. It should also serve as a basis for comparison of *Dicranoptycha* with other genera. Although McAlpine's terminology is probably desirable to facilitate phylogenetic comparisons of the Tipulidae with other families, the terminology used here is that of Byers (1961) because of its past use in tipulid taxonomy. The morphology of *Dicranoptycha megaphallus* is used here as representative of the genus and is similar to that of other North American species of *Dicranoptycha* unless otherwise stated.

Dicranoptycha is a genus of medium-sized crane flies within the tribe Limoniini. Characteristics that separate it from other Limoniini are: wings with vein R_2 lying far distad, beyond level of outer end of cell 1st M_2 (Fig. 6); a conspicuous pale fold in cell Cu (Fig. 6); and in males the rod-like lateral processes, one at the mesal side of each basistyle (Fig. 9). Body length varies from 7 to 13 mm; females are usually larger than males. Wing length is from 7 to 12 mm. The wings are unmarked in American species but may have a yellow or brown tinge. Body color varies from yellow to dark brown. There is no sexual difference in external morphology except for the terminal abdominal segments. Details of morphology are described by Young (1980). Only such information is presented here as is needed to clarify Figures 1-16.

Head. Lateral and ventral parts of the head largely occupied by dark compound eyes; eyes widely separated dorsally, close to each other ventrally; dorsal and lateral surfaces of head covered by long setae; antenna 16-segmented, filiform, arising on anterior part of vertex between eyes; scape cylindrical, three times as long as wide; pedicel globular, shorter, slightly wider than scape; flagellomeres subcylindrical, tapered apically, each with 4-6 verticillar setae near middle. Rostrum (Fig. 1) short, half length of head, with two conspicuous terminal labellar lobes; oral cavity formed by ventral hypopharynx and dorsal labrum; mandibles absent; maxillary galea situated below basal segment of maxillary palp.

Thorax. Neck membranous except for lateral cervical sclerite; prothorax and metathorax extremely reduced, mesothorax greatly developed (Figs. 4,5); pronotum short, convex, closely adjoining proepisternum laterally, proepimeron triangular above base of the fore coxa; mesonotum occupies nearly the entire dorsal thoracic region, distinctly divided into prescutum, scutum, scutellum and postscutellum (postnotum). Transverse suture abruptly deflected backward near mid-line and narrowly U-



FIGURES 1-4. *Dicranoptycha (D.) megaphallus*. 1, mouthparts, anterodorsal aspect. 2, distal end of hind leg, dorsal aspect. 3, distal end of hind leg, lateral aspect. 4, thorax, dorsal aspect. Abbreviations: ant-antenna, cl-claw, emp-empodium, gal-galea, hal-haltere, hyp-hypopharynx, lab-labellar lobe, lbr-labrum, mtn-metanotum, mxp-maxillary palp, pasc-parascutellum, prn-pronotum, psc-prescutum, psci-postscutellum, psf-pseudosutural fovea, rst-rostrum, scl-scutellum, scu-scutum, w-wing.

shaped (Fig. 4); prescutum large, gibbous, with a pair of pseudosutural foveae near anterolateral margins; scutum indistinctly divided medially into two portions, wings articulated beneath its lateral margins; scutellum separated from scutum by suture and with parascutellum at each side; caudal margin of the postscutellum extends over the metathorax. Mesopleuron divided by pleural suture into anterior mesepisternum and posterior mesepimeron, mesepimeron weakly divided into upper anepimeron and lower katepimeron, meron situated below mesepimeron; pleurotegrite situated at upper caudal margin of anepimeron, mesothoracic spiracles located in membranous area below prescutum and behind proepimeron. Metanotum small, beneath postscutellum, with narrow, visible lateral, transverse band; pleural suture extending from coxal process to base of haltere, dividing metapleuron into anterior metaepisternum and posterior metepimeron, metepimeron united dorsally with metanotum. Base of haltere between pleurotergite and metanotum. Metathoracic spiracle in front of base of haltere and below pleurotergite.

Wings elongate, strongly irridescent under light at certain angles. Membranous areas yellow or brown without darkened stigma, vein C darker, longitudinal veins except 2A covered with setae, wing margins fringed. Cells beyond cord long, cord located about one-third wing length from apex, fork of Rs well before cord, Rs with two branches, R_2 lying distad beyond level of outer end of cell 1st M_2 (Fig. 6); a clear, pale fold arises from near mid-length of first anal vein and runs toward and then parallel to margin of cell Cu. Haltere with cylindrical basal pedicel and bulbous, glabrous capitulum. Legs covered with numerous hairs, no distinct difference in length among legs; coxae of fore and middle legs broadly separated by mesothoracic episternum, coxae of middle and hind legs closely situated; trochanter short, densely sclerotized at distal margin with a sharp, black

spine directed inward into femur; proximal part of femur slanted, with ventral end longer than dorsal end; femur and tibia long, slender, tibia longer than femur; tarsus slender, five segmented, basitarsus the longest tarsomere, subequal to rest of tarsomeres, distal four tarsomeres darker than basitarsus; pretarsus with claws simple and a compressed, pulvilliform empodium (Figs. 2-3).

Male Abdomen. With nine evident segments (Fig. 7), first seven with spiracles, ninth segment highly modified in structure, ninth tergum and sternum fused into a nearly continuous ring with membrane at mid-ventral region, ninth tergum broadly and shallowly emarginate, tenth segment largely hidden beneath ninth tergum. Basistyles cylindrical, with two dististyles (Fig. 9), between ninth tergum and sternum, dorsal dististyle densely sclerotized, darkly pigmented, pointed at apex; ventral dististyle pale, stiferous and blunt at apex, both dististyles bend mesad, apices directed cephalad in resting position.

The male internal reproductive system includes a densely sclerotized apparatus lying mainly in the eighth and ninth abdominal segments (Fig. 10). The reproductive apparatus in *Dicranoptycha* is different from that of Tipulinae in two ways. First, it has a ventral rather than a dorsal position. Second, it does not rotate so as to give rise to the aedeagus from its anterior face as on Tipulinae; instead, the aedeagus is directed wholly caudad. Various apophyses pertaining to the aedeagus diversify greatly among the species and offer taxonomically useful characters.

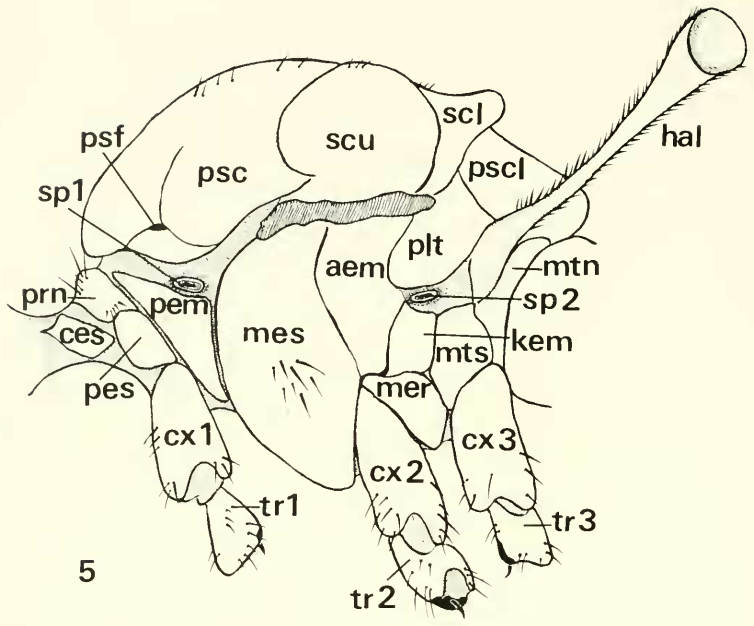
The main body of the male reproductive apparatus is the vesica, which lies ventrally in the ninth segment. The vesica (Figs. 11, 12) is a bulb-like structure with the opening of the seminal duct at its anterior end; it is connected to the aedeagus caudally. The massive, concave, dorso-ventrally depressed aedeagus protrudes from the abdominal cavity and lies in the cleft of the ninth sternum (Fig. 9,10). The aedeagal process (Fig. 12), which may be absent in some species, consists of two continuous parts attached to the aedeagus at its base. In *D. megaphallus,* the upper part is a lightly sclerotized, flat plate, darker at its posterior margin. The lower part is hook-like, attached first to the upper part at its anterior end, then the base of the aedeagus and lying medially above the aedeagus (Fig. 10). Both the aedeagus and its process are highly variable in shape among species but constant within a species.

Five immovable apodemes are attached to the vescia (Figs. 11,12). The anterior apodemes (dorsal apodeme, Starý, 1972) arise from the anterior end of the vesica and extend into the seventh segment, or in some species do not reach the seventh segment. They separate widely in *D. megaphallus* but form a single mesal apodeme in other species. The lateral apodemes are nearly uniform in structure throughout the genus. The upper part of each lateral apodeme extends upward and backward and forms the external, pale, rod-like, lateral process (Alexander, 1926) adjacent to the mesal base of each basistyle. The apex of the lateral process is somewhat triangular in cross-section and gives the impression of having three flat sides. The lateral process has been interpreted as tergal arm (Alexander, 1940), interbasal process (Alexander, 1926) and interbase (Starý, 1972). The lateral processes are connected dorsally by means of a narrow brace, or dorsal bridge, over the top of the vesica. The lower parts of the lateral apodemes extend ventrally around the vesica and meet at its mid-ventral line, where they fuse and form a well developed keel-shaped ventral apodeme which is vestigial in some species.

Female Abdomen. With ten visible segments (Fig. 8); first seven unmodified, last three shortened to form ovipositor; eighth tergum much reduced, eighth sternum well developed, projected backward below ninth and tenth segments, forming pair of basally fused hypovalves (Fig. 13); hypovalve concave on inner surface forming pocket with gonopore at anterior base; hypovalve with eight to twelve stiff bristles on inner dorsal edge; ninth tergum about same size as eighth, narrow lateral arms of ninth deflected caudad and joining ninth sternum, ninth sternum concealed by eighth sternum.

In *D. megaphallus,* the only sclerotized, externally visible reproductive apparatus that has an internal connection is the genital furca (Figs. 15,16), or fused redimentary gonapophyses (Snodgrass, 1903). It is found in the membranous area of the eighth sternum, directly below the aperture of the bursa copulatrix. The genital furca has its base above the oviduct at the base of the hypovalves, and its arms fuse with the bases of the ninth sternum (second vavulae). The tenth segment is elongated and tapered caudad. Strong blade-like cerci arise from the caudal margin of the tenth tergum. The shape of the cerci is used in this study as a characteristic to subdivide the genus into three species groups. The tenth sternum is only lightly sclerotized and bears long stiff setae at its caudal margin.

Two major internal reproductive structures can be seen through the side of a specimen cleared in potassium hydroxide. The common oviduct (Fig. 15) leads cephalad from the gonopore along the floor of the eighth segment to the bases of the hypovalves. In *D. megaphallus*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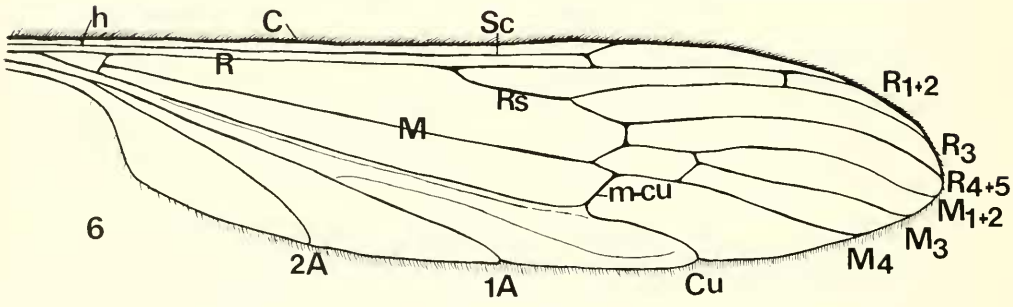
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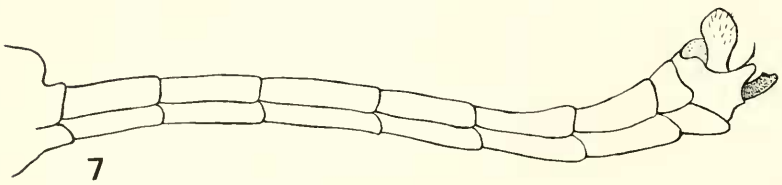

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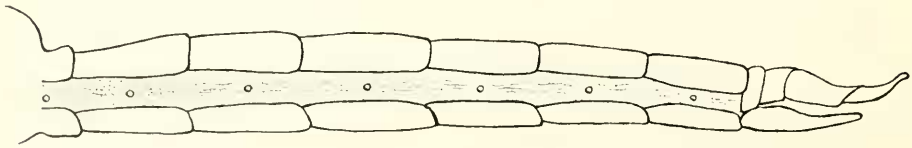

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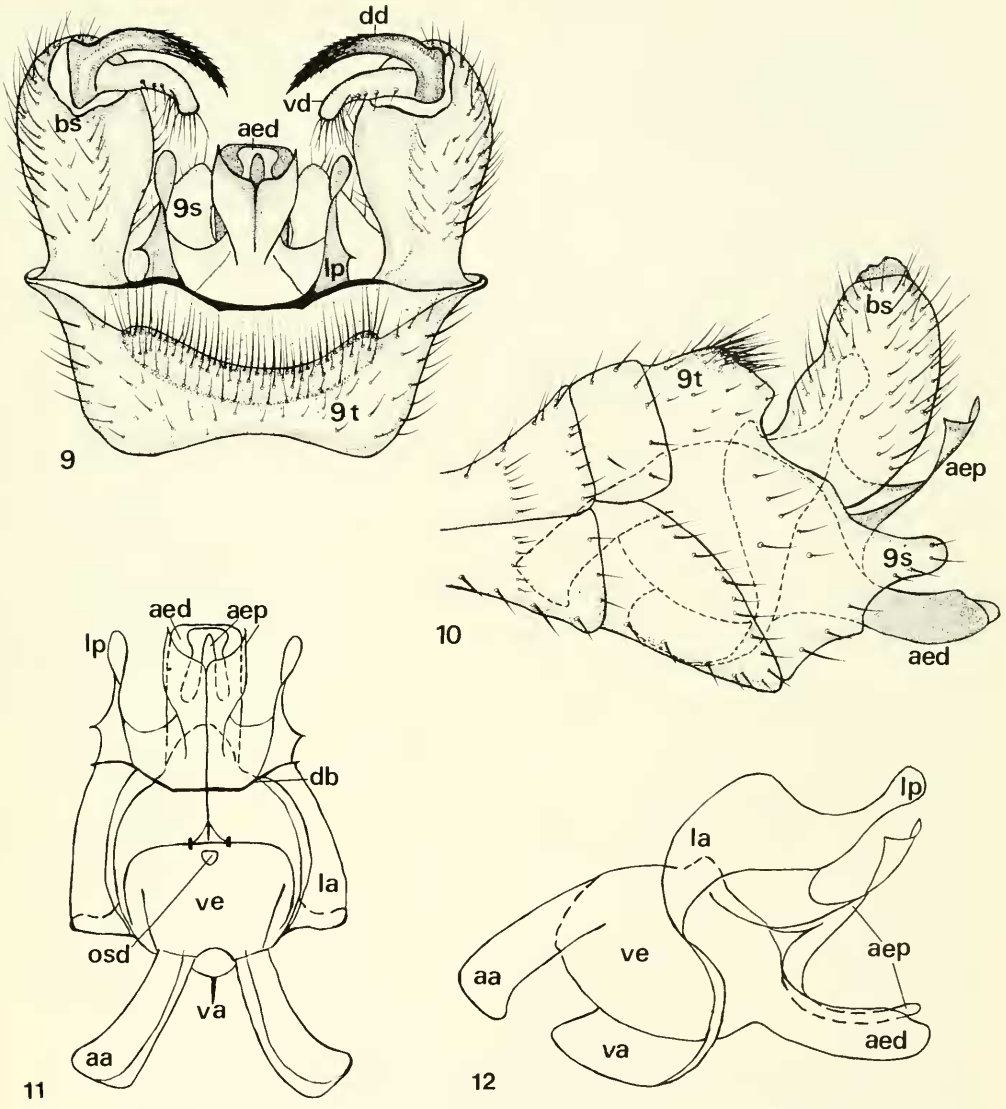
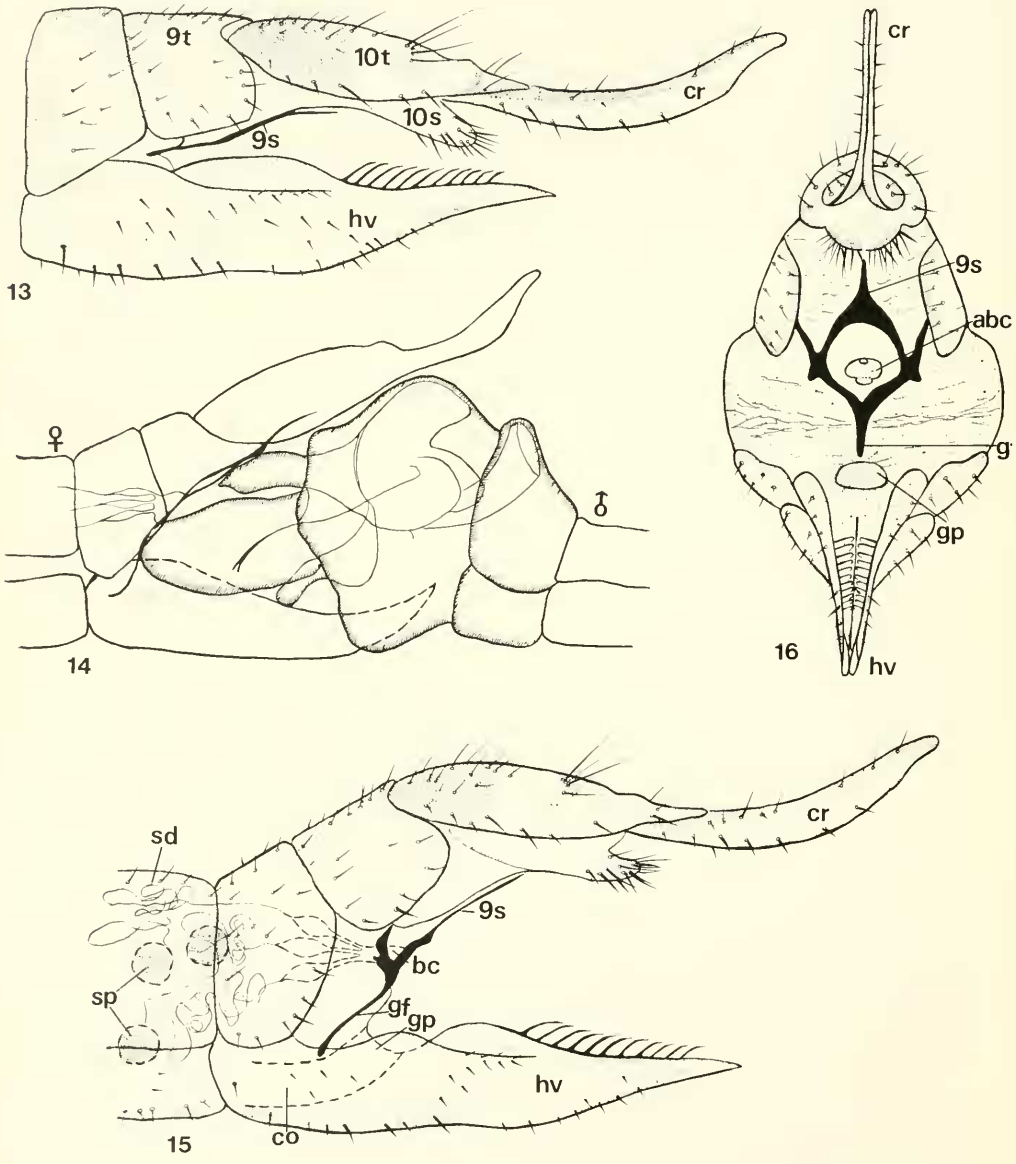


FIGURES 9-12. *Dicranoptycha (D.) megaphallus,* male hypopygium. 9, dorsal aspect. 10, left lateral aspect. 11, internal reproductive ystructures, dorsal aspect. 12, left lateral aspect. Abbreviations: aa-anterior apodeme, aed-aedeagus, aep-aedeagal process, bs-basistyle, db-dorsal bridge, dd-dorsal dististyle, la-lateral apodeme, lp-lateral process, osd-opening of seminal duct, s-sternum, t-tergum, va-ventral apodeme, vd-ventral dististyle, ve-vesica.

← FIGURES 5-8. *Dicranoptycha (D.) megaphallus.* 5, thorax, left lateral aspect. 6, wing. 7, male abdomen, left lateral aspect. 8, female abdomen, left lateral aspect. Abbreviations: A-anal veins, aem-anepimeron, C-costa, ces-cervical sclerite, cx-coxa, Cu-cubitus vein, h-humeral crossvein, hal-haltere, kem-katepimeron, M-media veins, m-cu-median cubital crossvein, mer-meron, mes-mesepisternum, mtn-metanotum, mts-metepisternum, pem-proepimeron, pes-proepisternum, plt-pleurotergite, prn-pronotum, psc-prescutum, pscl-postscutellum, psf-pseudosutural fovea, R-radius veins, Rs-radial sector, Sc-subcosta vein, scl-scutellum, scu-scutum, sp-spiracle, tr-trochanter, w-wing.

(Fig. 15), the short bursa copulatrix is formed by fusion of three greatly convoluted spermathecal ducts, each duct having a sac-like enlargement near the aperture of the bursa copulatrix and connecting to a spherical, darkly sclerotized spermatheca at its anterior end. The spermathecae is oval in some other species.

When females are examined from the postero-ventral aspect (Fig. 16), the ninth sternum (fused valvulae), genital furca, and aperture of the bursa copulatrix can be seen clearly. The first two parts are densely sclerotized and nearly uniform throughout the genus. The aperture of the bursa copulatrix is in the membranous area



FIGURES 13-16. *Dicranoptycha (D.) megaphallus*. 13, female hypopygium, left lateral aspect. 14, detail of hypopygia of male and female in mating. 15, female hypopygium, left lateral aspect showing internal reproductive structures. 16, female hypopygium, postero-ventral aspect. Abbreviations: abc-aperture of bursa copulatrix, bc-bursa copulatrix, co-common oviduct, cr-cercus, gf-genital furca, gp-gonopore, hv-hypovalve, s-sternum, sd-spermathecal duct, sp-spermatheca, t-tergum.

surrounded by the ninth sternum and genital furca. In *D. megaphallus* this aperture is wide at the level of the membrane but narrowed anteriorly, thus appearing as a rounded depression. In some other species, an additional structure, the receptacle for the male's aedeagal process, can be seen in this membraneous area. The slightly sclerotized receptacle for the aedeagal process is situated below the aperture of bursa copulatrix. The wall of this receptacle can be seen extended inward when one examines a specimen cleared in potassium hydroxide. The form of the receptacle varies among species and it is especially well developed in species in which the male has a complicated aedeagal process, such as *D. nigripes, D. pallida, D. tigrina.* The gonopore can be seen at the base of hypovalve, below the genital furca.

External Morphology of Immatures

The only published reference to immature stages of *Dicranoptycha* is that of Alexander (1919b), who recorded the larval habitat and morphology of two species, *D. pallida* (as *D. winnemana,* corrected by Alexander, 1926) and *D. minima.* Descriptions of immature stages of a third species, *D. megaphallus,* are contained in this section.

Egg. Matured egg oval, about 0.38 mm in length and 0.25 mm in width, soft and buff colored when laid, soon harder and brown. Chorion appears rough, covered with hexagonal protuberances (Fig. 17).

Last Instar Larva. Length 22-24 mm, dextrosinistral and dorsoventral diameters both 1.0-1.1 mm. Body form (Fig. 22) terete, strikingly elongate and vermiform. Integument transparent in life, white after preservation in alcohol. Body glabrous except for creeping welts consisting of 25-30 transverse rows of microscopic hooks on ventral surfaces of abdominal segments 2-8. Spiracles on pleura of abdominal segments 1-7, each with one small darkened sclerotized plate posterior to its sclerotized opening (Fig. 23).

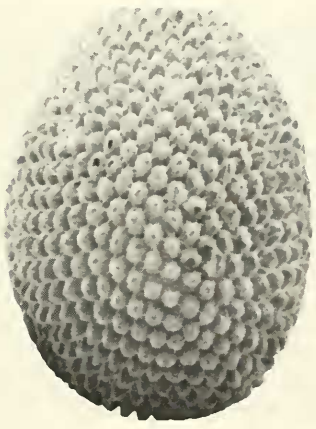


Figure 17. Egg of *Dicranoptycha (D.) septemtrionis.*

Head capsule (Figs. 18, 19, 20) sclerotized. Antennae two-segmented, inserted above bases of mandibles; basal segment elongate and cylindrical, about three times as long as basal width; apical segment slender, tapering apically, about half length of basal one. Labrum three-lobed (Fig. 18) with minute hairs anteriorly. Frontal suture distinct, darkly sclerotized; clypeus broad, pale. Mandible (Fig. 20) of cutting-chewing type, strongly sclerotized, with three, small, blunt teeth at apex and large molar area. Maxilla (Fig. 19) with sclerotized cardo and stipes, deeply cleft anteriorly between subequal inner lacinia and outer maxillary palp. Hypostomal bridge broad, heavily sclerotized, deeply cleft behind, with three bluntly rounded teeth. Hypopharynx with two sclerotized arms and rounded central part covered with microscopic tubercles.

Spiracular disk (Fig. 21) with four fleshy lobes, a lateral pair and a ventral pair; lateral lobes slightly longer than ventral ones. Spiracles small, fuscous brown with blackish centers, separated by distance slightly more than transverse width of a spiracle. Inner face of lateral lobe with brown mark of which pointed proximal end curves up toward spiracle. Ventral lobe bears smaller brown mark near base. Inverted Y-shaped brown mark on disk between lateral lobes. Anal gills inconspicuous, forming ring-like protuberance around anus.

The larva of *Dicranoptycha megaphallus* resembles that of *D. pallida,* differing most conspicuously in the structure of the hypostomal bridge. It lacks the basilateral notch in each lateral tooth.

Pupa. Length from cephalic crest to tip of abdomen 9.5-10 mm in male, 10-11 mm in female; diameter about 1.8 mm. Form (Figs. 24,25) terete, gradually tapering from base of wing pads to slender cauda. Pupa pale when young, older pupa with brown thorax and light yellow abdomen; structures of adult clearly visible through cuticle of older pupa. Pronotal respiratory horn very small, a tiny tubercle when viewed anteriorly or dorsally. Tips of wing sheaths reaching mid-length of third abdominal segment. Apices of sheaths of all tarsi reaching about end of fifth abdominal segment. Abdomi-

nal segments each subdivided into four transverse ridges dorsally and three ventrally, each ridge bearing transverse band of microscopic hooks. Spiracles on pleural regions of segments 2-7, behind each a patch of microscopic hooks. Cauda of both sexes with two schlerotized hooks curved dorsocephalad; hooks large and conspicuous in male (Fig. 26), smaller and projecting from near apices of cercal sheaths in female (Fig. 27). Male with additional pair of small projections near dorsolateral margin of ninth tergum; female hypovalves slightly larger than cercal sheaths.

BIONOMICS

ADULT. In North America adults of *Dicranoptycha* usually emerge in spring, but a few species emerge in summer or autumn. All species appear to have one generation a year. At the beginning of the emergence period, males are more abundant than females, and toward the end the females are more numerous. When the adults are raised in the laboratory, their life span is about six days; survival would probably be shorter in natural habitats. In Kansas, the season of flight for each species lasts about three weeks. The remainder of the year is passed as immature stages in the ground.

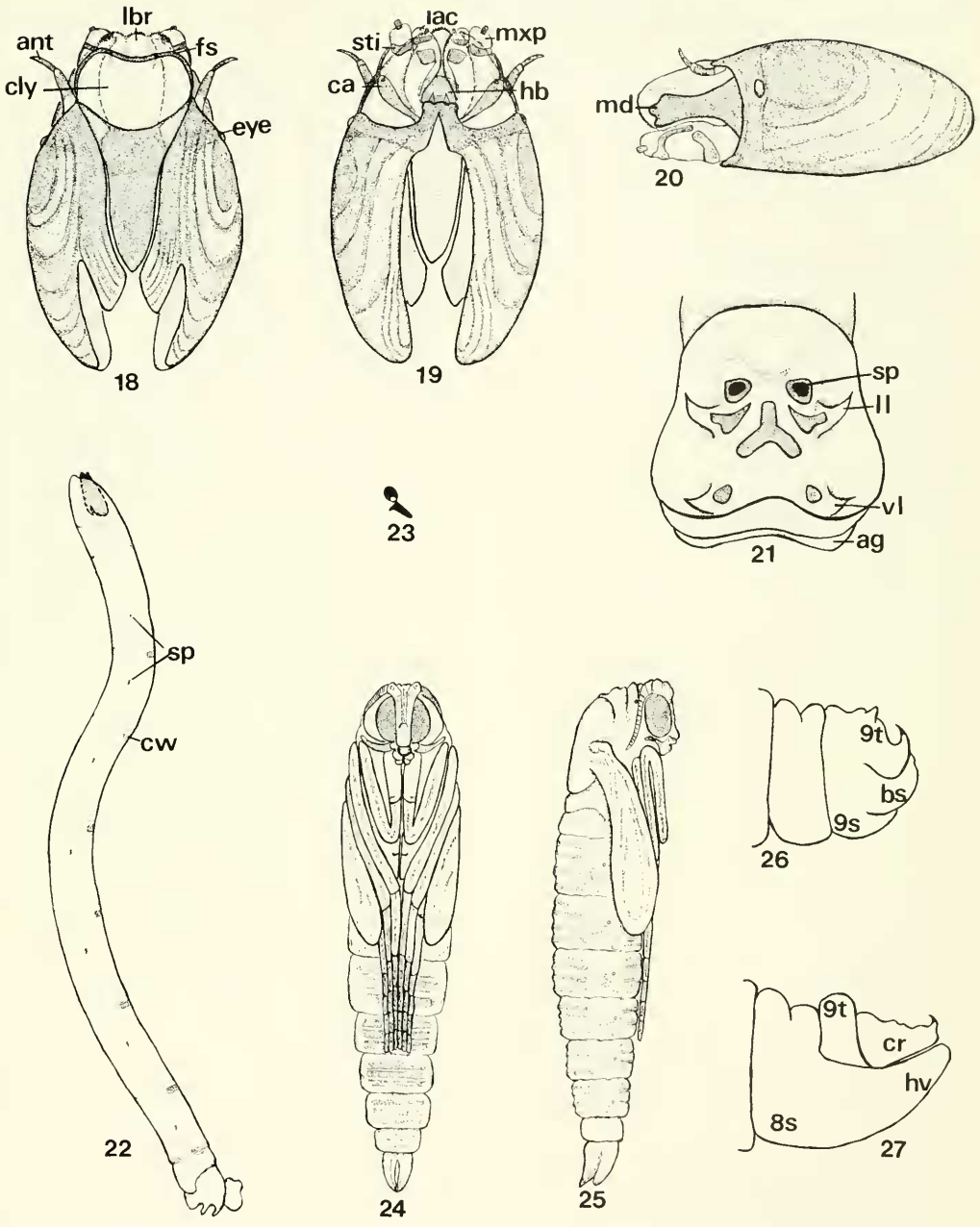
Net collecting indicates that adults occur in humid to relatively dry open woodlands, locally restricted to the undergrowth stratum of shrubs and herbs. In Kansas, Missouri, Illinois or other western parts of the eastern range of the genus, *Dicranoptycha* is associated with poison ivy, nettle, jewelweed, and buckbrush shaded by oak-hickory forests. Farther to the east, especially along the lower slopes of the Appalachians, the flies are associated with *Eupatorium,* bugbane *(Cimicifuga),* jewelweed, poison ivy and other undergrowth herbs of mixed deciduous forests of oak, maple and tulip tree. Species with a western distribution are most likely to be found in the undergrowth of evergreen forests but can also be found in the drier chaparral.

Adults usually stand upright, with the body elevated parallel to the upper surfaces of leaves and the wings folded flat over the back. The up-and-down bobbing motion seen in many other genera is inconspicuous. They are sluggish flies; when disturbed they fly about two meters before they alight. They apparently do not shift into higher or lower strata in response to diurnal changes in temperature, light intensity, humidity or combinations of these factors. Aggregations of individuals occur in the more favorable habitats, and in such places mating pairs can be found at any time of the day.

The main functions of the adults are mating and egg-laying. Feeding is less important, and probably water is the most pressing need. In the morning, adults can be found slowly walking on the upper surfaces of leaves, exhibiting rapid movements of the maxillary palpi in search of water. I have observed the adults drink from dewdrops. Sugar water was offered as food for adults kept in laboratory. Oviposition was not observed in the field. Egg-laying appears to take place at night when females can also be found walking or resting on the ground of the daytime habitats. In the laboratory, eggs were laid singly and scattered in the soil surface. In the natural habitat, eggs probably are laid in the leaf litter.

Seven species of *Dicranoptycha* were recorded from the vicinity of Lawrence, Kansas, where most of my biological observations were made. *D. megaphallus* is the first species to appear in May, followed by *D. elsa* and *sobrina* in June, *D. pallida* in July, and then the fall species, *D. septemtrionis, tigrina,* and *minima,* in September. *D. megaphallus* will serve as a representative of the genus.

IMMATURE STAGES. Larvae of *D. megaphallus* can be found in the soil of the habitat where the adults occurred earlier in the season. Larvae occur within two or three millimeters of the surface of the soil after the leaf litter has been removed. They are active and move freely through the soil without established burrows. The shiny, glassy appearance suggests that the body is probably covered by some secretion. Larvae feed on decayed plant material in the ground. In rearing dishes, all the feces are deposited on the top of the soil. The number of larval stadia is probably four but was not verified. In the wild, small, early stage larvae of *D. megaphallus* can be collected in November, and fully grown



FIGURES 18-27. *Dicranoptycha (D.) megaphallus,* immature stages. 18, head capsule of last instar larva, dorsal aspect. 19, ventral aspect. 20, left lateral aspect. 21, cauda of last instar larva. 22, last instar larva, left lateral aspect. 23, spiracle of last instar larva. 24, pupa, ventral aspect. 25, pupa, right lateral aspect. 26, cauda of male pupa. 27, cauda of female pupa. Abbreviations: ag-anal gill, ca-cardo, cly-clypeus, cr-cercus, cw-creeping welt, fs-frontal suture, hb-hypostomal bridge, hv-hypovalve, lac-lacinia, lbr-labrum, ll-lateral lobe, md-mandible, mxp-maxillary palp, s-sternum, sp-spiracle, sti-stipes, t-tergum.

ones in March. Judging from these collecting data, eggs probably hatch in May, a week or two after oviposition; larvae reach the fourth instar by fall, overwinter, and resume feeding in spring until pupation occurs in late April.

The mature larvae make horizontal tunnels about three millimeters under the soil surface. At the end of its tunnel the larva makes a small cell for pupation. The inside of the cell is smooth but without silk. The earthen walls of the cell are cemented, probably with saliva, and are quite firm and thick. The cell itself (with adhering earth particles) can be easily sorted out from loose soil. The cell is open at one end, slightly over one half the length of the mature larva, but large enough for the larva to move freely and make turns. At this stage larvae decrease in length by more than one-third. The duration of the pupal stage is about ten days. The adult emerges at night, pushing the earth from the open end of the pupal cell and freeing itself from the pupal skin. Usually the posterior two thirds of the pupal skin remains in the cell. Newly emerged adult flies rest on the ground before the first flight.

Mating Behavior

Several species of *Dicranoptycha* have been observed to form mating pairs at nearly any time of day during the peak season of adult emergence. No swarming behavior is known for species of this genus. In no case did I find mating to involve a teneral female; I therefore assume that males do not actively search for newly emerging females on the ground, as in several other genera. Direct body contact between two flies plays an important role in activity leading to copulation. Presumably, adults are attracted to the same shaded places in undergrowth vegetation and physical contact may occur in such places. Whether sexual or aggregation pheromones are involved in bringing the males and females together is unknown.

During mating, both flies stand high, with the body elevated and orientated parallel to the substratum, usually the upper surface of a leaf in low undergrowth. They face in opposite directions, the female maintaining her normal body position, while the male's abdomen turns 180 degrees and grasps the female genital segments from behind. The connection between male and female is secured by the male grasping the lateral membranous areas of the female's eighth segment with his dorsal and ventral dististyles, and by the insertion of the female's hypovalves into the male's genital chamber against the hidden tenth segment.

A distinct change from the ordinary position of the male internal reproductive structures can be observed during copulation. As a lateral view (Fig. 14) shows, the vesica rotates about 45 degrees, so that the anterior apodemes press against the ninth sternum. The ridge formed by the ventral apodeme pushes the cerci away from the hypovalves and exposes the aperture of the bursa copulatrix, where the male aedeagus is introduced. Although in some species the aedeagal process and the lateral processes do not perform any obvious function in mating, in *D. megaphallus* the aedeagal process is brought into close proximity to the gonopore of the female (Fig. 14).

When a resting pair is disturbed, they fly in a more or less straight descending line, with the male flapping his wings but being carried by the female until she alights on some object. The duration of mating is unknown. One mating pair of *D. megaphallus* reared in the laboratory remained in copulation for about nine hours. Another pair of the same species was collected *in copula* in their natural habitat and remained together for eight hours after being brought into the laboratory.

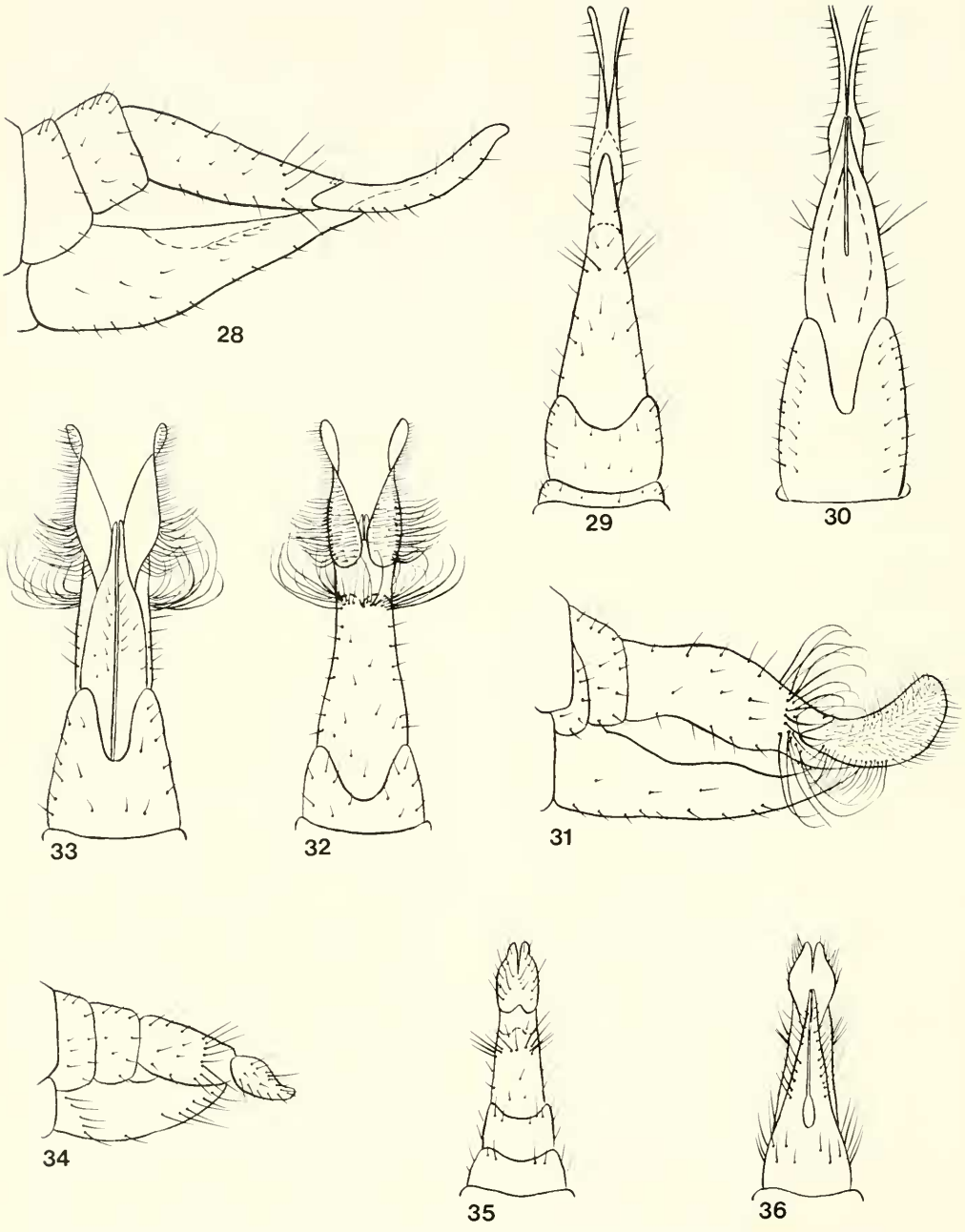
Subgenus *Dicranoptycha*

All North American species belong to the subgenus *Dicranoptycha,* in which three well-defined species groups can be recognized on the basis of the female cerci. The *germana* group consists of *D. acanthophallus, australis, byersi, elsa, germana, megaphallus, minima, nigripes, pallida, septemtrionis, sobrina, spinifera, tennessa, tigrina,* and *winnemana.* Females of this group have the cerci long and slender, blade-like, narrowly rounded or pointed apically, longer than or subequal to the length of the tenth tergum.

The cerci and tenth tergum are evenly covered by uniformly short setae, except ten to twelve longer ones near the posterior end of the tenth tergum (Figs. 28, 29, 30; these figures were drawn from a dried specimen, in which the cerci appear separated from each other in both dorsal and ventral aspects; in alcoholic specimens they are contiguous along the median line). The *melampygia* group includes *D. melampygia, nigrogenualis, occidentalis, quadrivittata, spinosissima* and *stenophallus*. The cerci of females of this group are short and broad, spatulate, shorter than the tenth tergum. The ventral margins of the basal half of the cerci flare out laterad. Long and dense setae form a partial whorl around the posterior end of the tenth tergum and along the flared margins of the cercal bases (Figs. 31, 32, 33; figures drawn from dried specimens). The *linsdalei* group contains only *D. linsdalei,* in which the cerci (Figs. 34, 35, 36) are very short, about one half the length of the tenth tergum. The bases of the cerci are fused together. Setae are evenly distributed on both the tenth tergum and cerci, with longer ones around the posterior end of tenth tergum. *D. laevis* is ungrouped in this study because the female is unknown to me.

Key to Adult Males of North American *Dicranoptycha*

1. Small species; body length about 6.5 mm or less 2
— Larger species; body length from 7 to 11 mm 4
2. Dorsal dististyle denticulate on outer curvature (Fig. 121). . . *linsdalei*
— Dorsal dististyle smooth on outer curvature (Figs. 61,125). 3
3. Ventral dististyle broadly expanded; aedeagus without processes (Figs. 61, 62) . . . . . *minima*
— Ventral dististyle not expanded; aedeagus with two conspicuous, blade-like aedeagal processes, recurved posteriorly to fuse with dorsum of aedeagus (Figs. 125, 126). . . . . *laevis*
4. Ninth sternum with short spines on posterior margin; vein 2A with setae (Figs. 53, 54) . . . . . *germana*
— Ninth sternum without spines on posterior margin; vein 2A without setae 5
5. Abdominal sterna bicolored 6
— Abdominal sterna unicolored. 8
6. Sterna each with anterior dark transverse band; aedeagus with undivided flattened aedeagal process (Figs. 77, 78) . . . . . *sobrina*
— Sterna each with dark transverse band between two light colored bands; aedeagus with two-branched aedeagal process (Figs. 65, 89) . . . 7
7. Body color reddish yellow; secondary branch arises from about midlength of aedeagal process (Figs. 65, 66) . . . . . *nigripes*
— Body color grayish brown; secondary branch arises from near tip of aedeagal process (Figs. 89, 90). . . . . *tigrina*
8. Lateral process with two arms (Figs. 113, 114). . . . . *spinosissima*
— Lateral process with single arm . . . 9
9. Lateral process with flange along outer margin of apical half (Figs. 97, 101, 105). 10
— Lateral process without flange . . . 12
10. Aedeagal process with rod-like lower part hanging behind aedeagus (Figs. 101, 102) . . . . . *nigrogenualis*
— Aedeagal process without lower part (Figs. 98, 106) 11
11. Body color grayish yellow; abdominal segments 7 and 8 forming darkened subterminal ring (Figs. 105, 106). . . . . *occidentalis*
— Body color brown; abdomen without subterminal darkened ring (Figs. 97, 98). . . . . *melampygia*
12. Body color yellow or brownish yellow 13
— Body gray or dark brown 17
13. Dorsal dististyle smooth on outer curvature; tips of femora and tibiae darkened (Figs. 69, 70) . . . . . *pallida*
— Dorsal dististyle denticulate on outer curvature; leg segments unicolorous 14
14. Abdominal segments 6 and 7 forming darkened subterminal rings; aedeagus conspicuous, dorso-ven-



FIGURES 28-30. *Dicranoptycha (D.) megaphallus,* female hypopygium showing typical cerci of germana group. 28, left lateral aspect. 29, dorsal aspect. 30, ventral aspect.

FIGURES 31-33. *Dicranoptycha (D.) melampygia,* female hypopygium showing typical cerci of melampygia group. 31, left lateral aspect 32, dorsal aspect. 33, ventral aspect.

FIGURES 34-36. *Dicranoptycha (D.) linsdalei,* female hypopygium. 34, left lateral aspect, 35, dorsal aspect. 36, ventral aspect.

trally flattened (Figs. 57, 58) . . . . . *megaphallus*

— Abdominal segment 7 forming darkened subterminal ring; aedeagus not as above 15

15. Aedeagal process with rod-like upper part, lower part enlarged and curved around three-branched aedeagus (Figs. 93, 94). . . *winnemana*

— Aedeagal process with flattened, broad upper part, lower part rod-like hanging behind short aedeagus (Figs. 42, 118) 16

16. Upper part of aedeagal process evenly rounded toward posterior margin in dorsal apsect (Figs. 117, 118) . . . . . *stenophallus*

— Upper part of aedeagal process abruptly rounded at about one-third of posterior end in dorsal aspect (Figs. 41, 42) . . . . . *australis*

17. Wings with a distinct brown seam along entire length of vein Cu . . . 18

— Wings without a brown seam along vein Cu 20

18. Aedeagus curved upward, with spines around edges (Figs. 45, 46) . . . . . *byersi*

— Aedeagus straight, with spines only at apex (Figs. 38, 82). 19

19. Aedeagus with spines at apex; lateral process as long as basistyle (Figs. 81, 82) . . . . . *spinifera*

— Aedeagus with tiny spines on inner apical surface; lateral process about half length of basistyle (Figs. 37, 38). . . . . *acanthophallus*

20. Aedeagus with two finger-like projections at posterior end; lateral process with pointed apex (Figs. 109, 110). . . . . *quadrivittata*

— Aedeagus without finger-like projections; lateral process with rounded apex. 21

21. Aedeagal process with upper part pale; lower part rod-like, bent ventrad; aedeagus with hook-like projection at posterior end (Figs. 73, 74). . . . . *septemtrionis*

— Aedeagal process with upper part darker at posterior margin; lower part rod-like, straight, aedeagus without projection. 22

22. Rod-like lower part of aedeagal process extending beyond aedeagus (Figs. 49, 50) . . . . . *elsa*

— Rod-like lower part of aedeagal process not extending beyond aedeagus (Figs. 85, 86). . . . . *tennessa*

Key to Adult Females of North American *Dicranoptycha*

1. Cerci short, broad, shorter than tenth segment; tenth tergum with score of long setae near posterior margin; flies of western North America. 2

— Cerci long, slender, subequal to or longer than tenth segment; tenth tergum with about 10-12 long setae near posterior margin (Figs. 28, 29, 30); flies of eastern North America . . . . . *germana* group 3

2. Cerci separate at bases and with long setae at slightly flared bases (Figs. 31, 32, 33); hypovalve with setae along inner dorsal edge . . . . . *melampygia* group. 17

— Cerci very short, fused at bases (Figs. 34, 35, 36), without long basal setae; hypovalve without setae on inner dorsal edge (Figs. 123, 124) . . . . . *linsdalei* group . . . . . *linsdalei*

3. Vein 2A with setae; postero-ventral aspect of external reproductive structure as in Fig. 56 . . . . . *germana*

— Vein 2A without setae 4

4. Abdominal sterna bicolored 5

— Abdominal sterna unicolored. 7

5. Sterna with dark transverse band at anterior part; postero-ventral aspect of external reproductive structure as in Fig. 80 . . . . . *sobrina*

— Sterna with dark transverse band between two light colored bands. . . 6

6. Body color reddish yellow; wing with yellow tinge; postero-ventral aspect of external reproductive structure as in Fig. 68 . . . . . *nigripes*

— Body color grayish brown; wing with gray tinge; postero-ventral aspect of external reproductive structure as in Fig. 92 . . . . . *tigrina*

7. Small species; body length about

6.5 mm or less; postero-ventral aspect of external reproductive structure as in Fig. 64 . . . . . *minima*
— Larger species; body length about 7-12 mm 8
8. Body color yellow or brownish yellow 9
— Body color gray or dark brown . . 12
9. Ninth sternum and genital furca separated (Figs. 72, 96) 10
— Ninth sternum and genital furca fused (Figs. 44, 60) 11
10. Legs yellow, tips of femora and tibiae darkened; receptacle for aedeagal process beneath aperture of bursa copulatrix (Fig. 72) . . *pallida*
— Legs yellow, without darkened tips on femora and tibiae; receptacle for aedeagal process beneath and around sides of aperture of bursa copulatrix (Fig. 96) . . . . . *winnemana*
11. Verticils long, about 2.5 times length of their respective flagellomeres; ninth sternum with angularly bent sides (Fig. 44). . . . *australis*
— Verticils about twice length of their respective flagellomeres; ninth sternum with evenly rounded sides (Fig. 60). . . . . *megaphallus*
12. Body color gray 13
— Body color dark brown. 14
13. Abdomen with darker terga and lighter sterna; body shorter than 10 mm; postero-ventral aspect of external reproductive structure as in Fig. 76 . . . . . *septemtrionis*
— Abdomen uniformly gray; body longer than 10 mm; postero-ventral aspect of external reproductive structure as in Fig. 88 . . . . . *tennessa*
14. Wings without a brown seam along vein Cu; postero-ventral aspect of external reproductive structure as in Fig. 52. . . . . *elsa*
— Wings with a distinct dark brown seam along vein Cu. 15
15. Ninth sternum and genital furca fused (Fig. 40) . . . . . *acanthophallus*
— Ninth sternum and genital furca separate (Figs. 48, 84) 16
16. Sides of ninth sternum straight (Fig. 48) . . . . . *byersi*
— Sides of ninth sternum rounder at basal half (Fig. 84) . . . . . *spinifera*
17. Ninth sternum and genital furca separated (Figs. 104, 116). 18
— Ninth sternum and genital furca fused 19
18. Body color dark brown; receptacle for aedeagal process present, beneath the aperture of bursa copulatrix (Fig. 104) . . . . . *nigrogenualis*
— Body color brown; receptacle for aedeagal process absent (Fig. 116) . . . . . *spinosissima*
19. Body color dark brown; postero-ventral aspect of external reproductive structure as in Fig. 100 . . . . . *melampygia*
— Body color gray or yellow 20
20. Body color gray; aperture of bursa copulatrix T-shaped (Fig. 112) . . . . . *quadrivittata*
— Body color yellow; aperture of bursa copulatrix rounded 21
21. Receptacle for aedeagal process present, beneath aperture of bursa copulatrix (Fig. 120) . . . . *stenophallus*
— Receptacle for aedeagal process absent (Fig. 108) . . . . . *occidentalis*

THE *GERMANA* GROUP

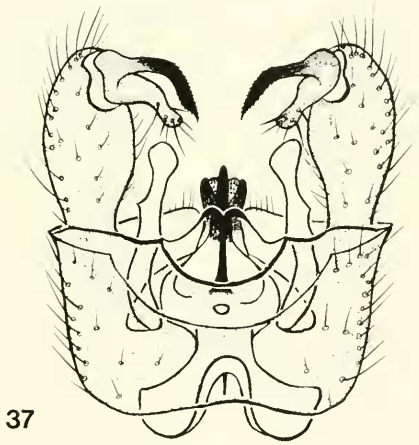
Dicranoptycha (Dicranoptycha) acanthophallus Alexander

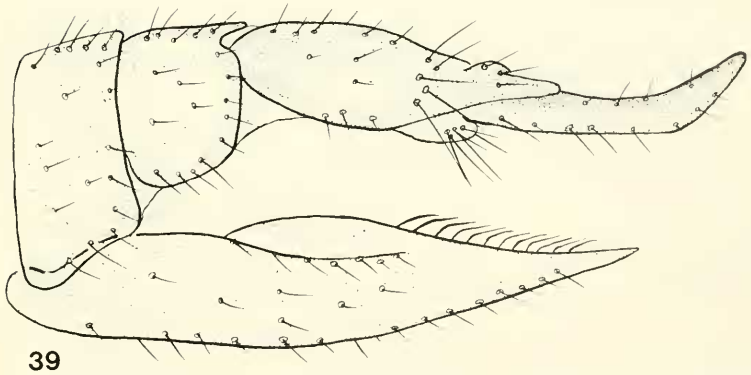
Dicranoptycha acanthophallus Alexander, 1940, Amer. Midland Nat. 24:621.

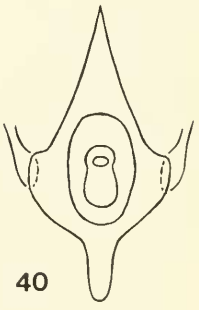
TYPES. Holotype, male, Gregory Ridge Trail, Blount County, Tennessee, 17 June 1939, C. P. Alexander. Allotype, same data as holotype. Paratypes, seven females, same data as holotype, one male and two females from Greenbrier Cove, Sevier County, Tennessee, 23 June 1940, C. P. Alexander. Holotype, allotype and nine paratypes are in the Alexander collection, NMNH. One female paratype is in UMMZ. The holotype and male paratype are mounted on microscope slides.

TAXONOMIC CHARACTERISTICS. Basic coloration dark brown. Male body length 8.5-9 mm, wing 10.5 mm. Female body length 9.5-11 mm, wing 12 mm. *Head* ashy gray, with one row of black bristles around each eye. Rostrum brown with slight gray pollinosity, palpi blackish brown. Antennal scape and pedicel tawny, flagellomeres dark brown. Verticils about twice the length of their respective flagellomeres. *Thorax* dark

brown with dense gray pollinosity on pleura. Mesonotum dark gray, prescutal stripes only weakly differentiated. Pseudosutural foveae polished black. Wings with yellowish brown tinge; a distinct brown seam along entire length of vein Cu; setae on all longitudinal veins except 2A. Halteres pale. Coxae yellow, pruinose at bases, trochanters yellow with black spot at ventral distal end, femora and tibiae yellow to testaceous with brown tips, basitarsi testaceous, tarsomeres dark brown. *Abdomen* slightly darker than thorax. Male hypopygium (Fig. 37) brownish yellow. Dorsal dististyle evenly curved and narrowed toward apex, abruptly narrowed only at tip and terminating in a straight spine; apical half blackened; spinules on apical half. Ventral dististyle strongly expanded at base, constricted before dilated apex. Male genitalia (Fig. 38) with vesica oval. Lateral process pale, expanded and rounded apically, with a sharp lateral point near base. Anterior apodemes slender at point of fusion with vesica, widening to broadly rounded apices. Upper part of lateral apodemes broadly expanded. Ventral apodeme keel-like, well developed. Aedeagus short and broad; about a dozen short, erect spines on dorsal concave surface at apex (visible by compound microscope). Aedeagal process small; upper part flat, plate-like, with two darker rounded lobes at posterior margin, connected beneath margin to hook-like lower part curved downward above aedeagus, its apex slightly exceeding tip of aedeagus. Female genitalia (Fig. 39) of *germana* form. Cerci about same length as tenth tergum, evenly narrowed toward tip, upturned a little beyond mid-length. Hypovalves reaching slightly beyond mid-length of cerci; twelve setae on inner dorsal edge of each hypovalve. Postero-ventral aspect of external reproductive structures as in Fig. 40.







Figures 37-40. *Dicranoptycha (D.) acanthophallus*. 37, male hypopygium, dorsal aspect. 38, left lateral aspect with external skeleton removed. 39, female hypopygium, left lateral aspect. 40, postero-ventral aspect.

COMPARATIVE NOTES. The general appearance of *Dicranoptycha acanthophallus* is similar to that of *byersi* and *spinifera,* while the male genitalia are somewhat similar to those of *elsa.* J. S. Rogers recorded in his study notes that "The Virginia specimens fit Alexander's description of male genitalia (as well as all other details) while the Ohio specimen is nearest the figure that accompanies description." After examining all these specimens, I have determined that those from Ohio are *D. elsa* and those from Virginia are *spinifera.* This confusion has resulted in most museum specimens determined as this species being actually *D. spinifera,* while most specimens of *acanthophallus* were found to be incorrectly determined as *elsa. D. acanthophallus* differs from *elsa* mainly by its generally shorter body and wings and darker color, the dark tips on the femora, the distinct brown seam along vein Cu, and in the male the shorter hook on the lower part of the aedeagal process, which in *elsa* extends far beyond the tip of the aedeagus. The similarities among *D. acanthophallus, byersi* and *spinifera* are discussed under *byersi.*

GEOGRAPHIC AND SEASONAL DISTRIBUTION. *D. acanthophallus* is known only from the southern Appalachian Mountains of Tennessee, North Carolina, and Georgia (Map 1). My collection records show that this species is most often taken with *D. byersi* and *spinifera* in valleys of 2000-3000 feet altitude, where woods of mixed tulip trees, oaks, maples, and white pine occur and undergrowth is jewelweed, greenbriar, and May-apple. All of the records for this species are in late May and June, suggesting that this is a late spring species. The captures indicate that the peak of emergence falls about the first week of June.

Summary of distribution: Georgia - Murray Co., 28 May; Towns Co., 30 May; White Co., 20 May. North Carolina - Haywood Co., 31 May. Tennessee - Blount Co., 17 June; Sevier Co., 23 June.

Dicranoptycha (Dicranoptycha) australis Alexander

Dicranoptycha australis Alexander, 1926, Psyche, 33: 55.

MAP 1. Known distribution of *Dicranoptycha acanthophallus* (triangles) and *D. australis* (circles). Each symbol indicates one or more county records.

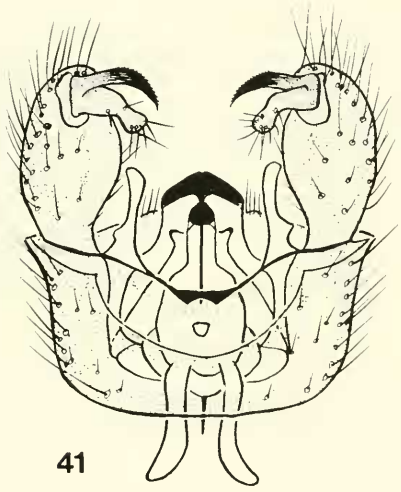
TYPES. Holotype, male, Gainesville, Alachua County, Florida, 15 April 1922, J. S. Rogers. Allotype, Ocmulgee Valley, Bibb County, Georgia, 3 June 1923, J. S. Rogers. Paratypes, four males and two females, same data as holotype; one male, same data as allotype. Holotype, allotype and most of the paratypes in UMMZ; two male paratypes in the collection of C. P. Alexander, NMNH. The holotype and three male paratypes are mounted on microscope slides.

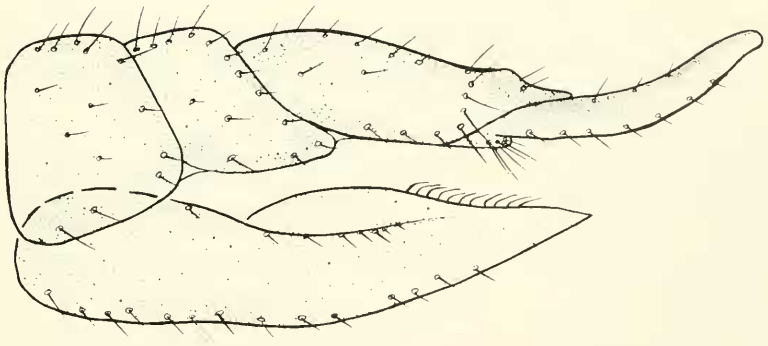
TAXONOMIC CHARACTERISTICS. Basic coloration brownish yellow. Male body length 8-8.5 mm, wing 8.5 mm. Female body length 8.5-9 mm, wing 9 mm. *Head* ashy gray, with one row of brown bristles around each eye. Rostrum brown, palpi dark brown. Antennae with dark brown scape, pedicel and flagellomeres brown. Verticils long, about 2.5 times length of their respective flagellomeres. *Thorax* brownish yellow, with gray pruinosity on all surfaces. Prescutum with grayish, poorly defined stripes. Pseudosutural foveae brown. Wings with brownish yellow tinge, costal fringe short, vein 2A without setae. Legs with coxae sparsely pruinose, trochanters, femora, and tibiae yellow, tarsomeres brown. *Abdomen* generally light brown; segment seven in male darker, forming dark subterminal ring. Male hypopygium (Fig. 41) yellowish brown. Dorsal dististyle evenly curved toward acicular apex, finely denticulate on outer curvature. Ventral dististyle with enlarged, rounded apex. Male genitalia (Fig. 42) with oval vesica. Lateral process reaching to about mid-length of basistyle, with apex directed slightly laterad. Anterior apodemes long and slender, separated at their bases. Lateral apodemes with lower part larger than upper

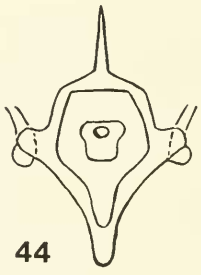
part. Ventral apodeme slender from both dorsal and lateral aspects. Aedeagus short, bent ventrad. Aedeagal process with broad, plate-like upper part, curved at sides and darker at posterior margin, connected posteriorly to median rod-like lower part hanging down behind aedeagus. Female genitalia (Fig. 43) of *germana* form. Cerci about same length as tenth tergum, evenly curved to slightly narrowed apex. Hypovalves reaching to about one-third length of cerci; eleven setae on inner dorsal edge of each hypovalve. In postero-ventral aspect of external reproductive structures (Fig. 44), ninth sternum fused with genital furca, sides of ninth sternum angularly bent.

COMPARATIVE NOTES. D. australis and *megaphallus* are similar to each other in having yellowish body color and a darkened subterminal ring on the abdomen in males. Males of these two species can be distinguished by the subterminal ring. In *D. australis* it is formed by the darkened seventh segment, while in *megaphallus* it is formed by darkening of both segments six and seven. Females of these two species can be separated by the form of the ninth sternum, which in the former has angularly bent sides and in the latter has rounded sides.

GEOGRAPHIC AND SEASONAL DISTRIBUTION. Collection records show that *D. australis* occurs from Indiana southward to central Florida, westward to Oklahoma (Map 1),







FIGURES 41-44. *Dicranoptycha (D.) australis.* 41, male hypopygium, dorsal aspect. 42, left lateral aspect with external skeleton removed. 43, female hypopygium, left lateral aspect. 44, postero-ventral aspect.

very closely approximating the range of *winnemana*. There is a four-month range of collection dates. Since the earliest date (15 April) was recorded from Florida and the latest date (26 August) was from Indiana, I believe that the difference in latitude accounts for this range and that *D. australis* has only one generation per year, as in the other nearctic species of the genus. The peaks of emergence differ locally; the collection records show May in Florida and August in Indiana.

Summary of distribution: Alabama - Baldwin Co., 14 May; Hale Co., 18 May. Florida - Alachua Co., 15 April, 10 May; Hamilton Co., 1 June; Marion Co., 29 May. Georgia - Bibb Co., 3 June; Burke Co., 30 June; Decatur Co., 8 June; Dooley Co., 1 June. Indiana - Jefferson Co., 31 July to 26 August. Missouri - Taney Co., 27 June. Oklahoma - Cleveland Co., 14 July; Pontotoc Co., 18 July. South Carolina - Abbeville Co., 27 June.

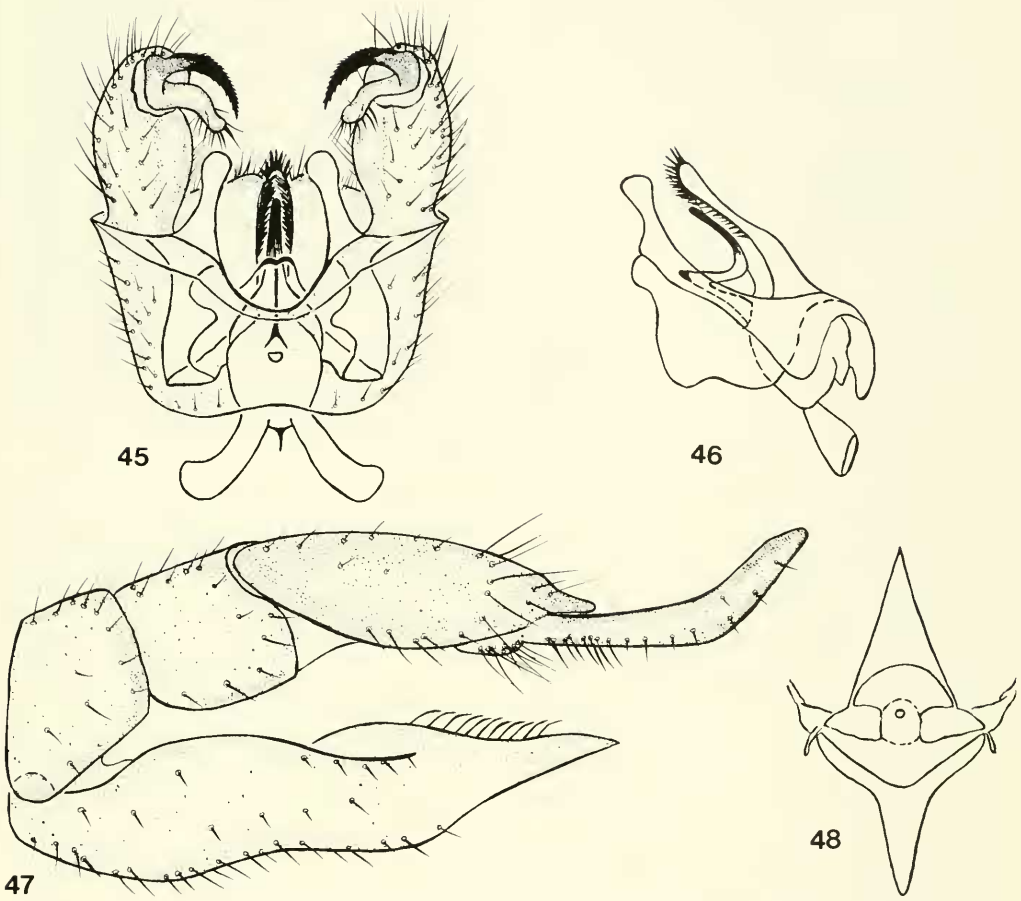
Dicranoptycha (Dicranoptycha) byersi, new species

TYPES. Holotype, male, Sunburst Forest Service Campground (10 miles southeast of Waynesville), Haywood County, North Carolina, 31 May 1978, G. W. Byers and C. W. Young. Allotype, same locality and date. Paratypes, 13 males and 3 females from the type locality, 31 May 1978, 1 male and 5 females from Morgan State Forest (4 miles north of Petros, 1850 feet) Morgan County, Tennessee, 1 June 1978. All types are in SEM. *Dicranoptycha byersi* is named in honor of Dr. George W. Byers, who discovered the habitat and helped collect the type series.

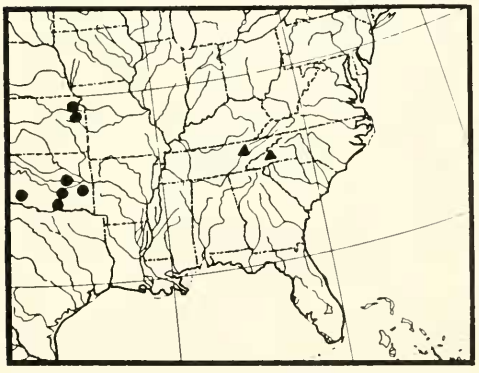
DESCRIPTION. Basic coloration dark brown. Male body length 8.5-9 mm, wing 10.5 mm. Female body length 9.5-11 mm, wing 12 mm. *Head* ashy gray, with one row of black bristles around each eye. Rostrum brown, pruinose; palpi blackish brown. Antennae with scape, pedicel and basal flagellomeres tawny, outer flagellomeres brown. Scape oblong, about twice as long as spherical pedicel. Flagellomeres oval, verticillate; dorsal verticils about twice as long as ventral ones, which just slightly exceed length of their respective segments. *Thorax* mostly dark brown, with gray pruinosity on pleurae. Mesonotum with light gold pruinosity, pseudosutural foveae polished black, longitudinal stripes on prescutum indistinct. Wings with ground color smoky yellow, a distinct brown seam along entire length of vein Cu. Veins testaceous, with setae on all longitudinal veins except 2A. Halteres pale throughout. Coxae tawny, bases of coxae pruinose. Trochanters yellow. Femora and tibiae yellow to testaceous with the brown tips, basitarsi testaceous, tarsomeres dark brown. *Abdomen* dark brown with light pollinosity. Male hypopygium (Fig. 45) brown. Dorsal dististyle evenly curved and narrowed toward apex, more abruptly curved at apex, both outer and inner curves denticulate. Ventral dististyle curved cephalad and with slightly enlarged apex. Male genitalia (Fig. 46) with vesica oval. Lateral process broadly expanded at tip. Anterior apodemes broad and separated from each other at their bases. Ventral apodeme small, keel-like. Aedeagus blade-like, curved upward from vesica with erect spines along entire edge. Aedeagal process complicated, with flat upper part, two lobed and darker at its posterior margin connected ventrally to upcurved, hook-like lower part situated medially above aedeagus. Female genitalia (Fig. 47) of *germana* form. Cerci slightly shorter than tenth segment, slightly broadened subapically, then tapered toward end. Hypovalves extending slightly beyond basal one-third of cerci; eleven setae on inner dorsal edge of each. Posteroventral aspect of external reproductive structures (Fig. 48) shows bases of ninth sternum extending into membranous area. Aperture of bursa copulatrix wide at level of membrane but narrowed anteriorly toward spermathecal ducts.

COMPARATIVE NOTES. D. byersi and *spinifera* are the only known species in which the aedeagus has spines that can be seen easily with a hand lens. In *D. byersi* the aedeagus curves upward and has spines all around the edge, while in *spinifera* the aedeagus is straight and bears spines only at the tip. In spite of the similarity of spiny aedeagi, these two species are not closely related, as indicated by the differences in all details of male genitalial structures (Figs. 45, 85). *D. byersi* is similar in its general appearance to *acanthophallus* but differs conspicuously in the structure of the male genitalia. The latter has a shorter, straight aedeagus (Fig. 37) and tiny spines on its inner surface that can be seen only with a compound microscope.

GEOGRAPHIC AND SEASONAL DISTRIBUTION. D. byersi is so far known only from two localities (Map 2). In both places, flies were



Figures 45-48. *Dicranoptycha (D.) byersi.* 45, male hypopygium, dorsal aspect. 46, left lateral aspect with external skeleton removed. 47, female hypopygium, left lateral aspect. 48, postero-ventral aspect.



MAP 2. Known distribution of *Dicranoptycha byersi* (triangles) and *D. minima* (circles).

collected with *D. acanthophallus* in hillside woods of tulip trees, maple, some oak and dogwood, where the shaded undergrowth included *Eupatorium,* jewelweed, poison ivy and bugbane. It seems likely that the range of *D. byersi* does not extend far west from these two localities, but it may occur in northern Georgia and elsewhere in the southern Appalachians. To judge from the collection dates and abundance of males at the time of collecting, *D. byersi* probably reaches peak abundance in the southern Appalachian region in late May and early June and can be described as a late spring species.

Dicranoptycha (Dicranoptycha) elsa Alexander

Dicranoptycha elsa Alexander, 1929, Bull. Brooklyn Entomol. Soc. 24: 28.

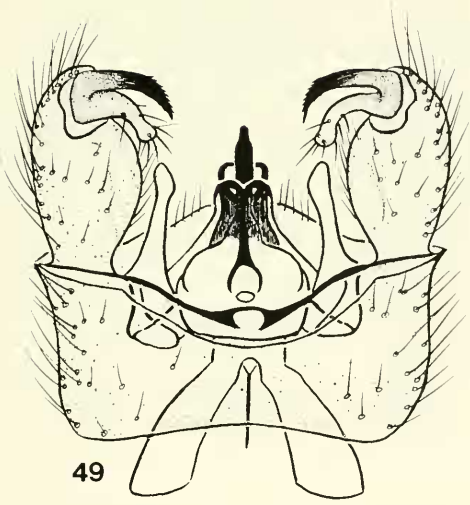
Types. Holotype, male, Tunesassa, Cattaraugus County, New York, 19 August 1926, C. P. Alexander. Allotype, same data as holotype. Holotype and allotype are in the collection of C. P. Alexander, NMNH. The holotype is mounted on a microscope slide.

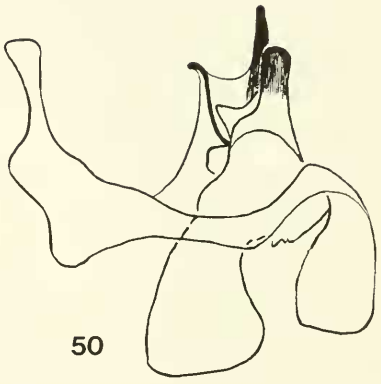
Taxonomic Characteristics. Basic coloration ochraceous to brown. Male body length 9.5-10.5 mm, wing 10 mm. Female body length 11-12 mm, wing 11.5 mm. (The female body length disagrees with that given in the original description, 10 mm. I measured twenty flies from three localities.) *Head* bluish ashy gray with one row of black bristles around each eye. Rostrum yellowish brown, palpi dark brown. Antennae with scape brown, pedicel brownish yellow, flagellomeres brown. *Thorax* dark brown with dense gray pruinosity. Mesonotum dark gray, prescutum with a broad brown stripe, which is indistinctly divided longitudinally by a narrow gray line at its posterior end. Pseudosutural foveae polished black. Wings infumed with yellow to testaceous, strongly iridescent under light from certain angles; vein 2A without setae, costal fringe short. Legs yellow to testaceous, tarsomeres dark brown. *Abdomen* darker than thorax, with light gray pruinosity. In male, segments six to eight more blackened. Hypopygium (Fig. 49) brownish yellow. Dorsal dististyle narrowed beyond mid-length toward acute apex; apical half roughened and denticulate. Ventral dististyle broad at base and curved before expanded apex. Male genitalia (Fig. 50) with vesica rounded. Lateral process extending to about mid-length of basistyle, apex slightly expanded. Upper part of lateral apodeme broadly expanded. Anterior apodemes large, separated to base, widely divergent. Ventral apodeme keel-like, well developed. Aedeagus short, thick, concave dorsally with a notch on upper posterior end. Aedeagal process complicated, upper part a flattened plate, darkened at posterior margin, connected to hook-like lower part posteriorly, lower part extended above and beyond tip of aedeagus. Female genitalia (Fig. 51) of *germana* form. Cerci about same length as tenth tergum, curved upward near mid-length and slightly broadened subapically, tips rounded. Hypovalves reaching to about mid-length of cerci; ten setae on dorsal inner edge of each hypovalve. Postero-ventral aspect of external reproductive structures as in Fig. 52.

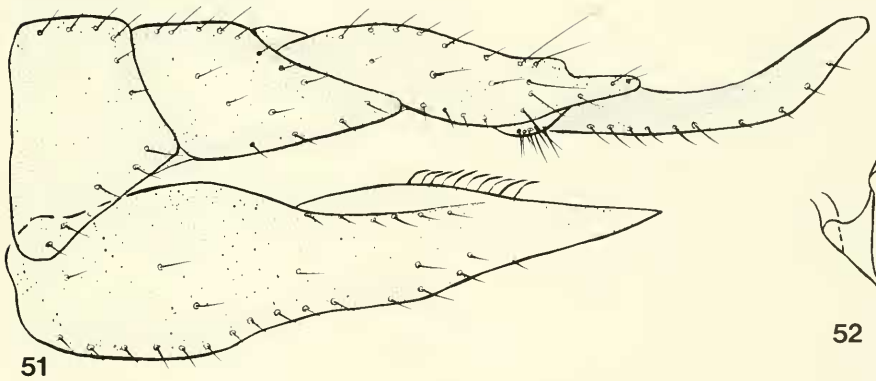
Comparative Notes. D. elsa is one of four dark brown species of the eastern species group. It can be easily recognized by lack of the dark brown seam along the Cu vein. The male of *D. elsa* is most likely to be confused with *acanthophallus*. Distinctions between these two species are included in the discussion of the latter. Alexander (1929) described the aedeagus as deeply split by an acute V-shaped notch. This was later illustrated in his Diptera of Connecticut (Alexander, 1942, Fig. 39D). Having examined the holotype and numerous other male specimens, I believe this described split is in the upper part of the aedeagal process as it appears on slide-mounted specimens.

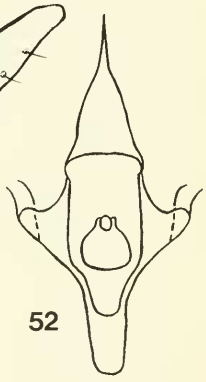
Geographic and Seasonal Distribution. Collection records show that *D. elsa* occurs from New York westward to eastern Kansas, and southward along the Appalachian Mountains to northeastern Georgia (Map 3). The distribution map shows a wide gap between the Kansas and eastern records; since suitable habitats exist within this gap, I believe further collection will prove that this species is more widespread in the eastern United States than present records indicate. In eastern Kansas the adults emerge from late May to mid June. Collection dates from Georgia, Ohio, North Carolina and Tennessee show peak emergence in mid June, indicating D. elsa is an early summer species. However, the August record from New York indicates that the peak

MAP 3. Known distribution of *Dicranoptycha elsa*.









Figures 49-52. *Dicranoptycha (D.) elsa.* 49, male hypopygium, dorsal aspect. 50, left lateral aspect with external skeleton removed. 51, female hypopygium, left lateral aspect. 52, postero-ventral aspect.

of emergence might be later in the northern part of the range.

Summary of distribution: Georgia - Towns Co., 21-30 May; White Co., 21 May. Kansas - Cherokee Co., 24 June; Douglas Co., 19 May to 11 June. New York - Cattarangus Co., 19 August. North Carolina - Avery Co., 1 June; Buncombe Co., 30 May. Ohio - Athens Co., 28 May; Hocking Co., 7 June. Tennessee - Fentress Co., 2 June; Morgan Co., 1 June. Virginia - Botetourt Co., 19 June; Rockbridge Co., 4 June.

Dicranoptycha (Dicranoptycha) germana Osten Sacken

Dicranoptycha germana Osten Sacken, 1859, Proc. Acad. Nat. Sci. Philadelphia, 1859: 217.

Types. Osten Sacken described *Dicranoptycha germana* from eight male and nine female specimens collected near Trenton Falls, Oneida County, New York, in July 1858. Of these original 17, one male and three female syntypes are in MCZ. The female types are darker than the male. The remaining syntypes could not be found.

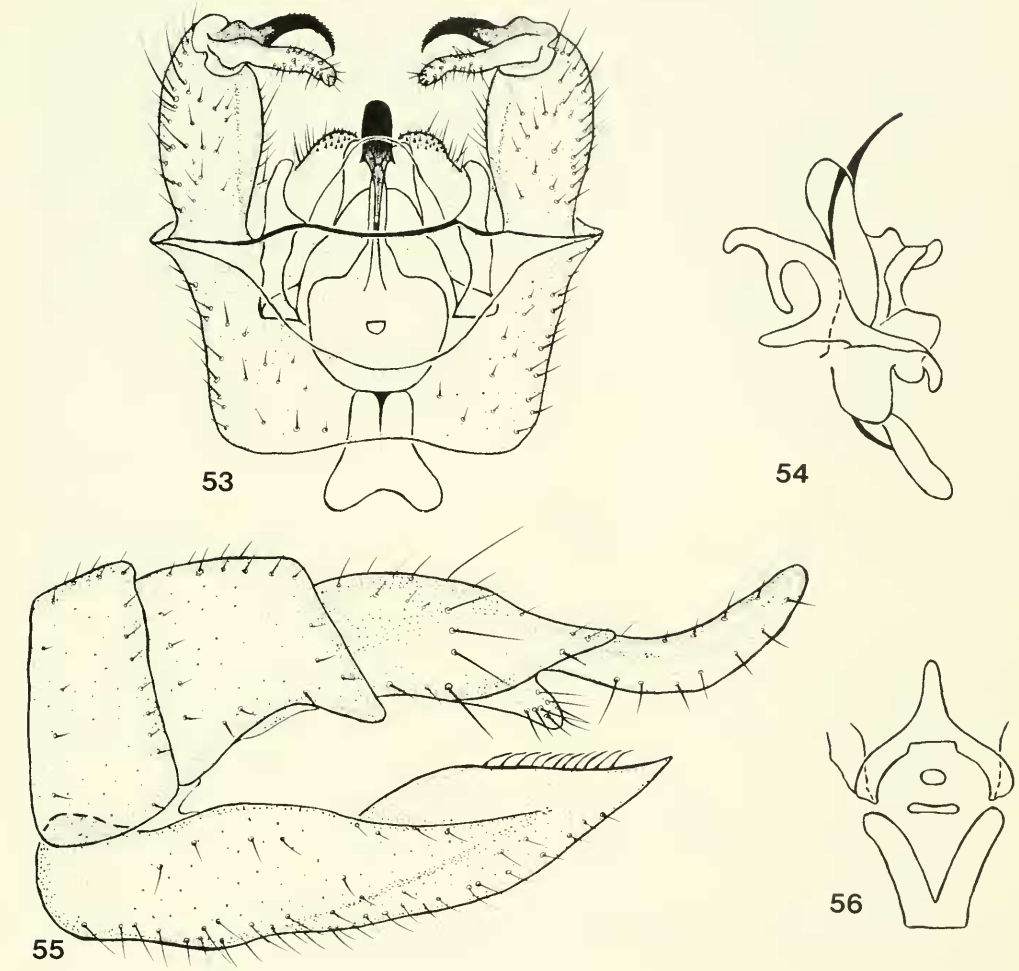
Taxonomic Characteristics. Basic coloration brownish yellow to reddish brown. Male body length 8-9.5 mm, wing 10-11 mm. Female body length 8.5-9.5 mm, wing 10-11.5 mm. *Head* cinereous, densely covered with long dark brown bristles. Rostrum brown, palpi blackish brown. Antennae with scape, pedicel tawny, flagellomeres brown. Verticils twice as long as their respective flagellomeres. *Thorax* varies from

tawny to brown with gray pruinosity on pleura. Mesonotum with brownish gray tinge, without longitudinal stripes. Pseudosutural foveae reddish brown. Wings with strong reddish brown tinge, with golden yellow setae on all longitudinal veins, costal fringe long and conspicuous. Halteres brownish yellow throughout. Legs uniformly testaceous in light colored individuals, only tarsomeres brown; in dark color phase, legs uniformly brown except bases of femora brown. *Abdomen* with terga uniformly reddish brown, sterna varying from tawny to reddish brown. In male, seventh and eighth segments form dark brown subterminal ring, hypopygium brown, posterior end of ninth sternum (gonapophyses, Alexander 1942) covered with short dark spines. Male hypopygium (Fig. 53) with dorsal dististyle tapering evenly toward apex, outer surface and apical inner surface denticulate. Ventral dististyle slightly arcuate, covered with setae. Male genitalia (Fig. 54) with vesica oval. Lateral process short, extending to about one-third length of basistyle. Anterior apodemes fused at mid-line, forming bilobed structure with dorsal crest at base. Ventral apodeme vestigial. Aedeagus short, inconspicuous, with bilobed end. Aedeagal process with upper part pale, flat, rounded at posterior margin, connected medially below to darkly sclerotized, tongue-like lower part curved ventrad. Female genitalia (Fig. 55) with blade-like cerci, about same length as tenth segment. Cerci slightly broadened at mid-length and slightly rounded toward tips. About a dozen long setae around mid-length of tenth tergum. Hypovalves not reaching mid-length of cerci, eleven setae on inner dorsal margin of each hypovalve. Posteroventral aspect of external reproductive structures as in Fig. 56.

Comparative Notes. This species shows striking variation in body color, from dark reddish brown individuals to light brownish yellow ones. The dark colored flies may be easily identified by their reddish brown wings and body. Specimens of the light color phase resemble *D. pallida,* but in that species the femora, tibiae and tarsomeres have dark tips, whereas these dark tips are absent in *D. germana. D. germana* also has a more hairy appearance than any other nearctic *Dicranoptycha.* Besides its conspicuous coloration, this species is distinct from the others in having setae on vein 2A and males with clusters of spines on the posterior end of the tenth sternum. Color variation in this species is independent of geographic distribution or ecological factors. Both color phases have been collected in the same habitats at various localities. The variation could be related to age, but more observations are needed to verify this hypothesis. Alexander (1942) described the costal fringe of *D. germana* as relatively short; he probably compared it with *sobrina* which has a longer costal fringe. Also in his figure (1942, Fig. 39E) the structure labelled as aedeagus is actually the tongue-like upper part of the aedeagal process. He also indicated the tips of the lateral process as acute in both his description and figure. I have examined many individuals and find them quite blunt.

Geographic and Seasonal Distribution. *D. germana* is known from Quebec westward to northern Minnesota and southward to South Carolina (Map 4). This is, so far as known, the only species of this genus that inhabits the Canadian life-zone. All the other species are characteristic of the Transitional and Austral life-zones. A series collected by J. Speed Rogers at Mountain Lake, Virginia, shows that this species emerges in late May and continues on the wing through mid-August, with a peak in mid-June. In the northern part of its range, *D. germana* emerges in June and disappears in October, with the peak in July.

Summary of distribution: Maryland - Garrett Co., 4 July; Montgomery Co., 5 July; Prince Georges Co., 29 May to 14 June. Michigan - Antrim Co., 2 July; Cheboygan Co., 26 July; Clare Co., 3 July; Gogebic Co., 24 July to 3 August; Lake Co., 22-26 June; Marquette Co., 13, 14 July; Osceola Co., 20 June; Washtenaw Co., 5 July. Minnesota - Clearwater Co., 11 July. New Hampshire - Grafton Co., 6 July. New York - Erie Co., 7 September; Essex Co., 5 August; Herkimer Co., 19 July; Oneida Co., 15 July; Tompkins Co., 20 July. North Carolina - Avery Co., 1 June. Ohio - Hocking Co., 4 October. Pennsylvania - Luzerne Co., 6 June. Quebec - Brome Co., 12 July, 2 September; Kamouraska Co., 5 July, 7 October. South Carolina - Spartanburg Co., 1 June. Virginia - Bath Co., 1 July; Fairfax Co., 6



Figures 53-56. *Dicranoptycha (D.) germana.* 53, male hypopygium, dorsal aspect. 54, left lateral aspect with external skeleton removed. 55, female hypopygium, left lateral aspect. 56, postero-ventral aspect.

June; Giles Co., 25 May to 15 August; Page Co., 15 July. West Virginia - Randolph Co., 5 July; Tucker Co., 3 July.

Dicranoptycha (Dicranoptycha) megaphallus Alexander

Dicranoptycha megaphallus Alexander, 1926, Psyche, 33: 57.

Type. Holotype, male, Allardt, Fentress County, Tennessee, at light, altitude 1650 feet, 10 June 1924, J. S. Rogers. The holotype is in UMMZ. The hypopygium is mounted on a microscope slide, and the remainder is pinned. The head and thorax of the type are greasy and the color has turned dark.

Taxonomic Characteristics. Basic coloration yellow. Male body length 9-9.5 mm, wing 9 mm. Female body length 9.5-10 mm, wing 10 mm. *Head* yellow, with one row of yellowish bristles around each eye. Rostrum and palpi brownish yellow. Antennae with scape, pedicel and basal four flagellomeres yellow, outer flagellomeres brownish yellow. Verticils about twice length of their respective flagellomeres. *Thorax* yellow with brownish yellow pruinosity on all surfaces. Prescutum with darker color along mid-line forming one brownish longitudinal

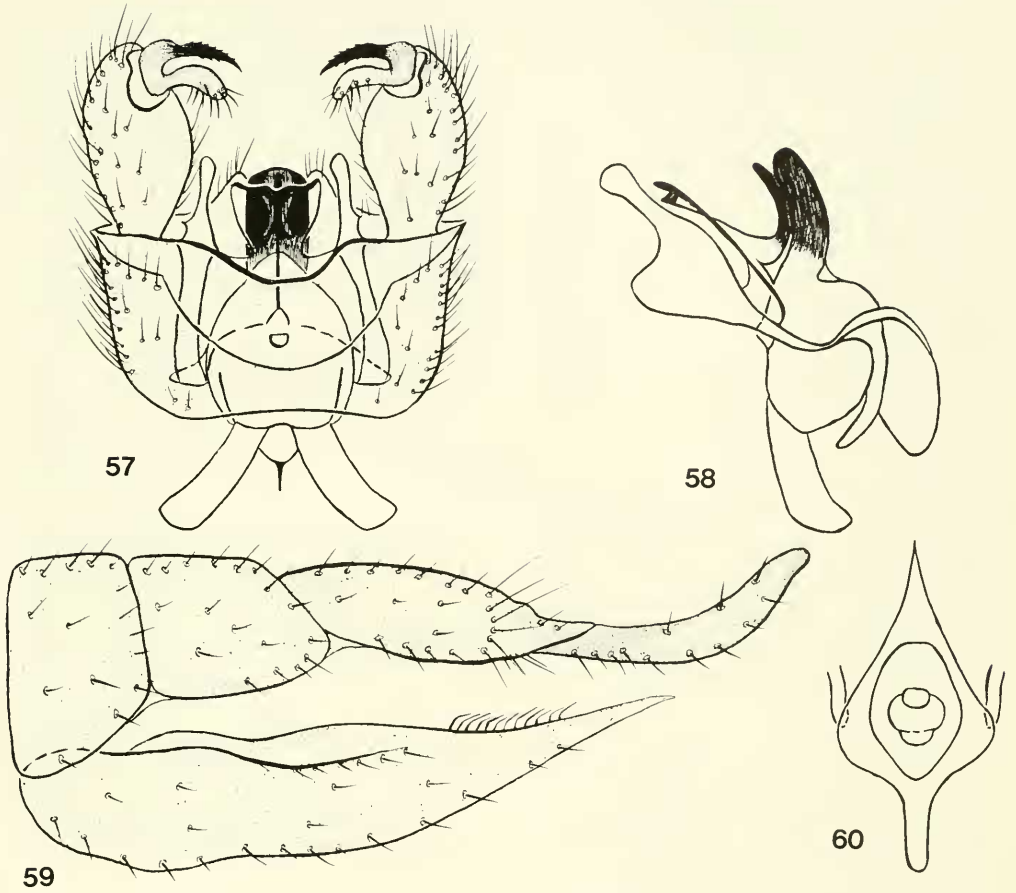
MAP 4. Known distribution of *Dicranoptycha germana.*

stripe. Pseudosutural foveae brown. Wings with yellow tinge, strongly iridescent, costal fringe short, vein 2A without setae. Legs yellow; outer tarsomeres brownish. *Abdomen* brownish yellow. Male with segments six and seven dark brown, forming broad subterminal ring. Male hypopygium (Fig. 57) yellow. Dorsal dististyle slender beyond slightly enlarged basal portion, evenly curved toward blackened, acicular apex, with denticulation on both outer and inner surfaces. Ventral dististyle slightly sclerotized, constricted near base. Male genitalia (Fig. 58) with large oval vesica. Lateral process reaching to about mid-length of basistyle. Lateral apodeme with both upper and lower parts expanded. Anterior apodemes conspicuous, elongate, and widely divergent from base. Ventral apodeme keel-like, well developed. Aedeagus conspicuous, large, dorso-ventrally flattened, with broadly rounded apex. Aedeagal process of *sobrina* form, with flattened, plate-like upper part, darker at posterior margin, connected anteriorly to hook-like lower part lying above aedeagus and narrowly connected to its sides. Female genitalia (Fig. 59) of *germana* form. Cerci about same length as tenth segment, evenly curved upward, with narrowly rounded apices. Hypovalves reaching to about mid-length of cerci; twelve setae on inner dorsal edge of each hypovalve. Postero- ventral aspect of external reproductive structure as in Fig. 60.

COMPARATIVE NOTES. D. megaphallus is closely related to *sobrina* and *tennessa* on the basis of male genitalial characteristics. Dr. J. S. Rogers recorded in his study notes that "*sobrina, megaphallus,* and probably *tennessa* are very close, probably geographic, ecological or other variants of one species." However, the distinct coloration of each species will at once separate them. The male genitalia also provide reliable specific characters. Regardless of the specific name of *D. megaphallus, sobrina* has the largest aedeagus, then *tennessa* and *megaphallus.* There also are differences in the attachment of the lower part of the aedeagal process to the aedeagus. In *D. sobrina* and *tennessa,* the junction of these two structures is at the base of aedeagus, while in *megaphallus* it is about one-third the length of the aedeagus from the base. Furthermore, the sympatric occurrence of these three forms supports the view that they are full species.

GEOGRAPHIC AND SEASONAL DISTRIBUTION. D. megaphallus ranges from western Virginia southward to Florida and westward to the Ozark Mountains and eastern Kansas (Map 5). Although the species has a generally southern distribution, it probably ranges farther north than present collection records indicate. There is one male reported from Ohio (Foote, 1956), but since I have not been able to verify the identification, it is not shown on the map. In northern Florida, Rogers (1933) found that *D. megaphallus* frequents the herb and shrub strata of high hammocks, upland woods, and clay hill woods. The flight period indicated in that study was 11 to 27 April in the years 1933 through 1936. In eastern Kansas this is the first species of the genus to emerge and has a flight period from late May to mid June. Collection dates from Illinois and Missouri also show dates around mid June. Accordingly, *D. megaphallus* appears to be a spring to early summer species, depending on latitude.

Summary of distribution: Alabama - Hale Co., 3 May. Arkansas - Marion Co., 15-16 May; Washington Co., 27 May. Florida - Jackson Co., 12-21 April; Jefferson Co., 18 April; Leon Co., 16-23 April; Liberty Co., 11 April. Georgia - Fulton Co., 21 May. Illinois - Randolph Co., 2



Figures 57-60. *Dicranoptycha (D.) megaphallus.* 57, male hypopygium, doral aspect. 58, left lateral aspect with external skeleton removed. 59, female hypopygium, left lateral aspect. 60, postero-ventral aspect.

June. Kansas - Cherokee Co., 7-13 June; Douglas Co., 21 May to 17 June; Franklin Co., 27 May; Johnson Co., 7 June; Labette Co., 2 June; Morris Co., 14 June; Pottawatomie Co., 14 June; Riley Co., 7 June. Kentucky - Christian Co., 3 June. Louisiana - Caddo Parish, 8 May. Missouri - Barry Co., 13-18 June; Camden Co., 1 June; Carter Co., 6 June; Laclede Co., 13 June; Taney Co., 10 June. Oklahoma - Adair Co., 15-17 June; Delaware Co., 19 June; Mayes Co., 18 June; Rogers Co., 6-19 June. Tennessee - Fentress Co., 10 June; Greene Co., 18 June. Virginia - Giles Co., 4 June.

MAP 5. Known distribution of *Dicranoptycha megaphallus.*

Dicranoptycha (Dicranoptycha) minima Alexander

Dicranoptycha minima Alexander, 1919, Entomol. News, 30: 21.

Types. Holotype, male, Lawrence, Douglas County, Kansas, altitude 900 feet, 16 July 1918, C. P. Alexander. Allotype, same data as holotype. Paratypes, 50 male and female, 11 September 1917. Twenty-two male and eight females paratypes are together with the holotype and allotype in the collection of C. P. Alexander, NMNH. Six male and two female paratypes are in UMMZ. Two male paratypes are in SEM. I have not been able to locate the other 10 paratypes. The holotype and three male paratypes are mounted on microscope slides.

Taxonomic Characteristics. General coloration brownish yellow. Male body length 6 mm, wing 6-6.5 mm. Female body length 6.5 mm, wing 6.5 mm. *Head* brown with golden pruinosity, one row of dark bristles around each eye. Rostrum brown, palpi dark brown. Antennae brownish black. Verticils long, about twice length of their respective flagellomeres. *Thorax* brownish yellow. Prescutum light borwn without longitudinal stripes. Pseudosutural foveae brown, pleura with light gray pruinosity. One distinct black spot at low end of pleural suture on mesothorax. Wings with strong brownish tinge, costal fringe short, inconspicuous. Legs with coxae yellow, heavily pruinose, trochanters yellow, femora and tibiae yellow with distinctly dark brown tips, tarsomeres dark brown. *Abdomen* yellowish brown without darker subterminal ring. Male hypopygium (Fig. 61) yellow. Dorsal dististyle smooth, broad at base and narrowed at about mid-length toward pointed tip. Ventral dististyle short, broad, setiferous. Male genitalia (FIg. 62) with vesica longer than wide; lateral process, short extending to about one-third length of basistyle. Both upper and lowers parts of lateral apodeme narrow. Anterior apodeme about same width as vesica at its base, broader at anterior margin, with shallow notch. Ventral apodeme small, keel-like. Aedeagus small, bilobed at posterior margin, with hook-like structure in front of each lobe; all these four projections bend ventrad. Aedeagal process absent. Female genitalia (Fig. 63) of *germana* form. Cerci about same length as tenth tergum, narrow at base, slightly widened just beyond mid-length, narrowed to upcurved tip. Hypovalve reaching to about mid-length of cerci; twelve setae on inner dorsal edge of each hypovalve. Postero-ventral aspect of external reproductive structures as in Fig. 64.

Comparative Notes. D. minima is the smallest species in the eastern species group. The only other species that it might be confused with is *D. septemtrionis,* but they may be distinguished by the dark brown tips of the femora and tibiae, and the smooth rather than denticulate dorsal dististyles of *D. minima.*

Geographic and Seasonal Distribution. D. minima is rarely seen in museum collections. I have seen specimens only from Kansas and Oklahoma and cannot verify the record for Illinois (Alexander, 1942). *D. minima* probably has a central plains distribution (Map 2). All but one of the collection dates are in September. The date for the holotype and allotype is in July. It is possible that Alexander described this species from laboratory-reared adults, which he mentioned emerged over a month earlier than the first individual taken in the field (Alexander, 1919b:68). *D. minima* is a late-summer to early-fall species.

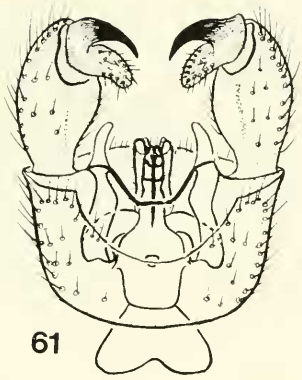
Summary of distribution: Kansas - Douglas Co., 16 July and 11 September; Jefferson Co., 15 September. Oklahoma - Kiowa Co., 3 September; Latimer Co., 26 September; Love Co., 7 September; Okfuskee Co., 4 September; Pontotoc Co., 6 September.

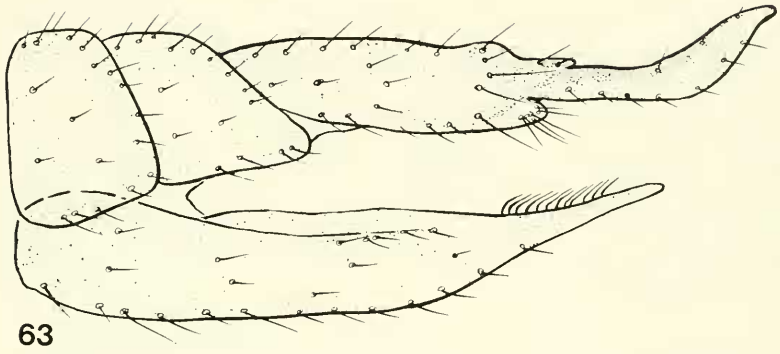
Dicranoptycha (Dicranoptycha) nigripes Osten Sacken

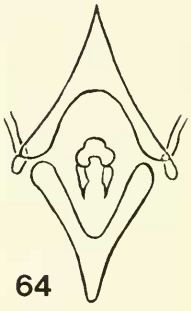
Dicranoptycha nigripes Osten Sacken, 1859, Proc. Acad. Nat. Sci. Philadelphia, 1859: 218.

Type. The original description was based on a male collected at Dalton, Whitfield County, Georgia, in 1859, by Osten Sacken; no more detailed data were mentioned. This type specimen is MCZ. It has intact body and wings but is without legs; one broken leg is attached to the determination label.

Taxonomic Characteristics. General coloration reddish yellow. Male body length about 10.5 mm, wing 9.5 mm. Female body length about 10.5 mm, wing 9.5 mm. *Head* ochraceous, with one row of dark brown bristles around each eye. Rostrum brown, palpi dark brown. Antennae black in male; in female, basal two segments yellow, flagellomeres brown. Verticils short, about same length as respective flagellomeres. *Thorax* reddish yellow, with strong pruinosity on all surfaces. Prescutum



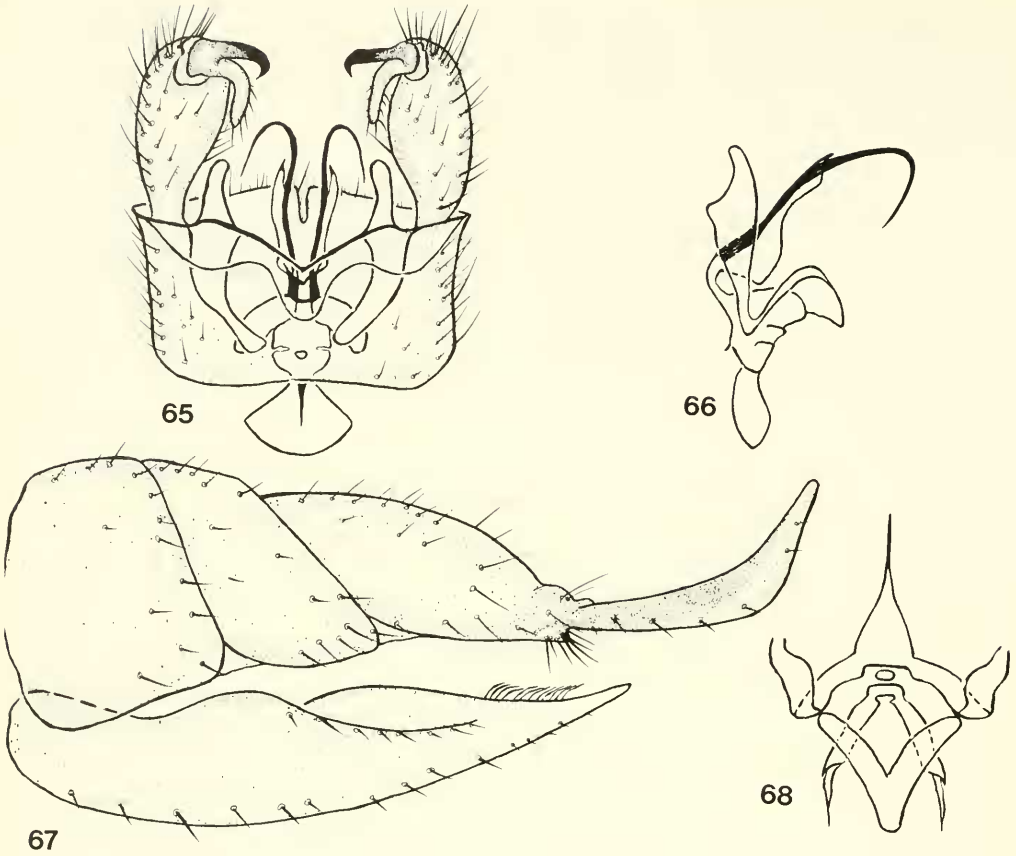




Figures 61-64. *Dicranoptycha (D.) minima.* 61, male hypopygium, dorsal aspect. 62, left lateral aspect with external skeleton removed. 63, female hypopygium, left lateral aspect. 64, postero-ventral aspect.

with one obscure median longitudinal stripe. Pseudosutural foveae reddish brown. Wings ferruginous, darker along anterior border, without setae on 2A, costal fringe short. Legs with coxae slightly pruinose, remainder of leg tawny, tips of femora and tibiae dark brown, tarsomeres dark brown. *Abdomen* brownish yellow, sterna three to seven with transverse blackened band near mid-length. In male, segment eight with blackened subterminal ring. Male hypopygium (Fig. 65) yellow, with ninth tergum deeply notched, margin of lobes with long conspicuous dark setae (omitted in figure). Dorsal dististyle abruptly narrowed and arcuate just before acute tip, outer curve glabrous. Ventral dististyle distinctly longer than dorsal one, strongly arcuate before mid-length, narrowed toward blunt tip. Male genitalia (Fig. 66) with small vesica. Lateral process broad at base and narrowed toward evenly rounded tip on both dorsal and lateral aspects. Lateral apodeme narrowed at middle, both upper and lower parts widened. Anterior apodeme single, without evidence of fusion of two apodemes, fan-like, narrow at base and widely expanded anteriorly. Ventral apodeme keel-like, well developed, about same size as anterior apodeme. Aedeagus short, inconspicuous. Aedeagal process (male forceps, Osten Sacken 1869) with two long, slender, dark structures branching out from base of aedeagus and bent ventrad, each branch with paler, thicker, darkly tipped secondary branch at about mid-length. Female genitalia (Fig. 67) of *germana* form. Cerci about as long as tenth segment, broadened beyond mid-length, tapered toward acute, upwardly curved tips. Hypovalves reaching slightly beyond base of cerci; twelve setae on inner dorsal edge of each hypovalve. Postero-ventral aspect of external reproductive structures (Fig. 68) shows inverted V-shaped receptacle for aedeagal process visible in membranous area below the aperture of bursa copulatrix.

Comparative Notes. In general appearance, *D. nigripes* resembles *sobrina* and *tigrina,* particularly in having banded abdominal sterna. The close similarity of



FIGURES 65-68. *Dicranoptycha (D.) nigripes.* 65, male hypopygium, dorsal aspect. 66, left lateral aspect with external skeleton removed. 67, female hypopygium, left lateral aspect. 68, postero-ventral aspect.

color is discussed under *D. sobrina.* In hypopygial structure of the male, *D. nigripes* most closely resembles *tigrina,* particularly in having a branching aedegal process. It differs from the latter species at first sight by its larger size and more reddish coloration. Close examination of the male genitalia confirms this separation. In *D. nigripes* the secondary branch arises from about mid-length of the aedeagal process, while in *D. tigrina* it arises close to the tip.

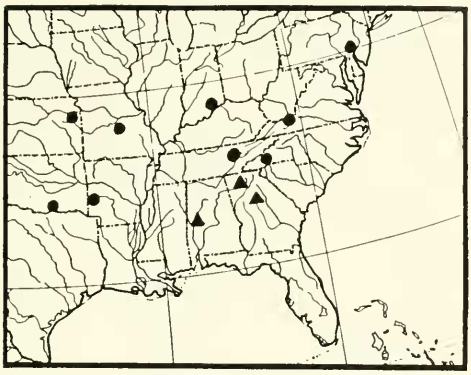
GEOGRAPHIC AND SEASONAL DISTRIBUTION. D. nigripes is so far known from only three localities, including the type locality in northwestern Georgia; Rogers' collection added two more records in western Alabama and central Georgia (Map 6). Absence of *D. nigripes* from the more northern Appalachians is possibly due to the fact that suitable habitats are occupied by the most closely related species, *D. tigrina.* Collection dates show that *D. nigripes* is probably a late-summer species.

Summary of distribution: Alabama - Hale Co., 18 July. Georgia - DeKalb Co., 16-25 August; Whitfield Co. (date unknown).

Dicranoptycha (Dicranoptycha) pallida Alexander

Dicranoptycha pallida Alexander, 1926, Psyche, 33: 58-59.

TYPES. Holotype, male, Lawrence (North Hollow, on the campus of the University of Kansas), Douglas County, Kansas, 1 August 1918,



MAP 6. Known distribution of *Dicranoptycha nigripes* (triangles) and *D. tigrina* (circles).

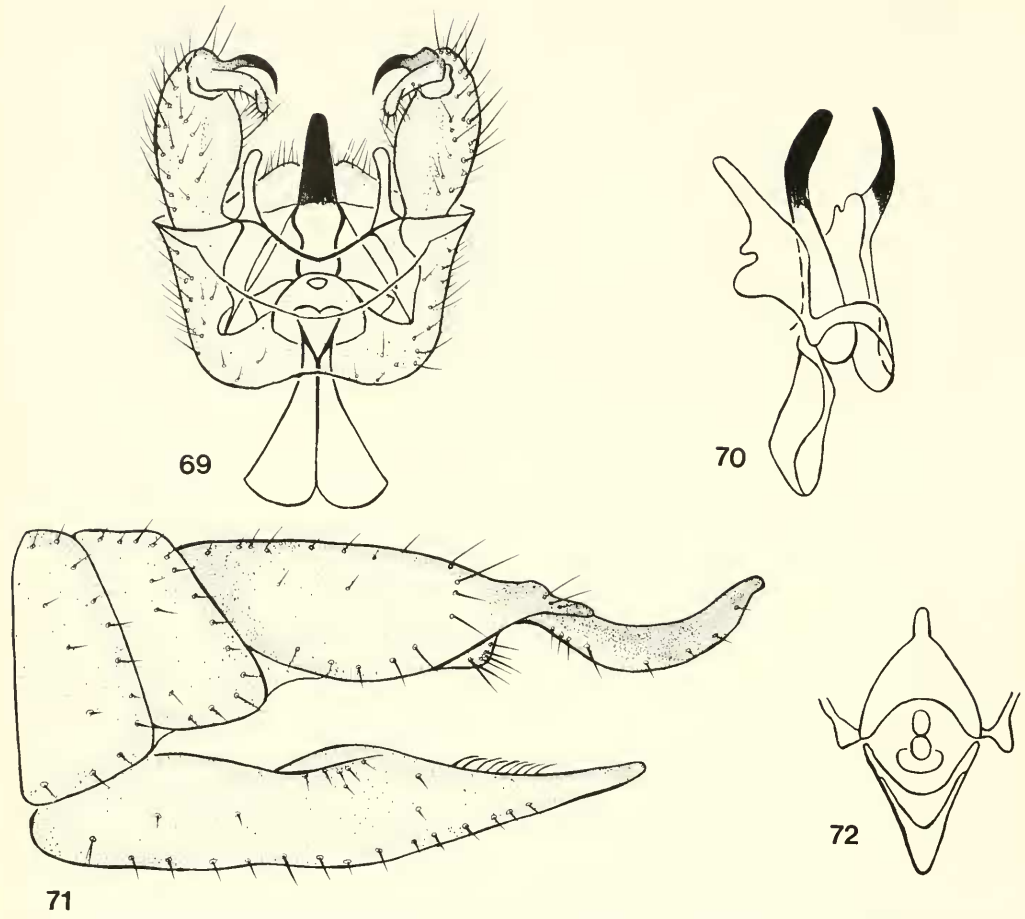
C. P. Alexander. Allotype, same locality and collector, 16 July 1918. Paratypes, four males and six females from the type locality, dated between 16 July and 1 August 1918. Holotype, allotype and most of the paratypes are in the collection of C. P. Alexander, NMNH. Two male and one female paratypes are in the UMMZ. The holotype and two male paratypes are mounted on microscope slides.

Taxonomic Characteristics. Basic coloration tawny. Male body length 7.5 mm, wing 8.5 mm. Female body length 9 mm, wing 9.5 mm. *Head* brownish yellow, with two rows of brown bristles around each eye. Rostrum brownish yellow, palpi brown. Antennae with scape, pedicel and basal four flagellomeres obscure yellow, outer flagellomeres infuscated. Verticils about twice as long as their respective flagellomeres. *Thorax* brownish yellow, with light gray pruinosity on pleura. Prescutum shiny brownish yellow, without longitudinal stripes. Pseudosutural foveae indistinct. Wings with strong brownish yellow tinge, with setae on all longitudinal veins except 2A; costal fringe short. Legs with coxae slightly pruinose, tronchanters obscure yellow, femora, tibiae and basal four tarsomeres yellow with darkened tips, apical tarsomeres brown. *Abdomen* with brownish yellow terga and pale yellow, slightly pruinose sterna. In male, segment seven conspicuously dark brown, eighth segment and hypopygium light yellow. Hypopygium (Fig. 69) with dorsal dististyle glabrous, evenly curved and narrowed toward apex. Ventral dististyle long, curved cephalad, narrowed toward blunt apex. Male genitalia (Fig. 69) with vesica rounded posteriorly. Lateral process extending to about midlength of basistyle. Lateral apodemes narrowed in lower part, upper part expanded. Anterior apodemes fused nearly their full length, about two and one-half times length of vesica, narrow at base, and separated by notch anterior margin. Ventral apodeme small, keel-like. Aedeagal process rod-like, dark in color and bent ventrad above dark, slender, tapering, upcurved aedeagus. Female genitalia (Fig. 71) of *germana* form. Cerci shorter than tenth segment, broadened near one-third length from base, then narrowed toward tips. Hypovalves reaching to about midlength of cerci; nine setae on inner dorsal edge of each hypovalve. Postero-ventral aspect of external reproductive structures (Fig. 72) with receptacle for aedeagal process beneath aperture of bursa copulatrix and receptacle for aedeagus above it.

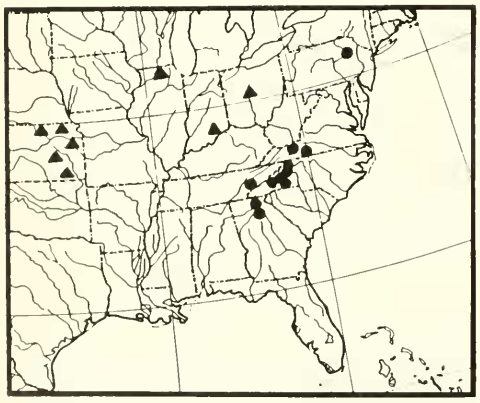
Comparative Notes. Both sexes of *D. pallida* can be identified in the field by the conspicuously darkened tips of the femora, tibiae and tarsomeres. This character separates this species from the otherwise similar *D. winnemana.* Male specimens are readily distinguishable by their unique aedeagus and aedeagal process. Together, these structures form a pincers configuration in lateral aspect. Alexander (1926) mentioned that he had confused *D. winnemana* with this species in the following papers: 1919a,b; 1920a. The aedeagal process (gonapophysis, Alexander 1926) and aedeagus in Alexander's original figure of this species appear to be side by side in a horizontal plane rather than the former above the latter, as they occur anatomically. This effect is probably due to the fact that the specimen was slide-mounted.

Geographic and Seasonal Distribution. *D. pallida* has been found in northern Illinois, Ohio, southern Indiana and eastern Kansas (Map 7). It was not found in any of the collections of Rogers or Byers from more eastern or southeastern states. Collection dates show that *D. pallida* is a midsummer species. In eastern Kansas *D. pallida* has a flight period from late June to mid July, with the peak of emergence in early July.

Summary of distribution: Illinois - Winnebago Co., 16 July. Indiana -Jefferson Co., 27 July to 1 August. Kansas - Douglas Co., 24 June to 16 July; Harvey Co., 2 July; Jewell Co., 22 July; Montgomery Co., 29 June; Nemaha Co., 5 July. Ohio - Delaware Co., 4 September.



FIGURES 69-72. *Dicranoptycha (D.) pallida.* 69, male hypopygium, dorsal aspect. 70, left lateral aspect with external skeleton removed. 71, female hypopygium, left lateral aspect. 72, postero-ventral aspect.



MAP 7. Known distribution of *Dicranoptycha pallida* (triangles) and *D. spinifera* (circles).

Dicranoptycha (Dicranoptycha) septemtrionis Alexander

Dicranoptycha septemtrionis Alexander, 1926, Psyche, 33: 56.

Dicranoptycha microphallus Alexander, 1947, Entomol. News. 57: 249 (new synonymy).

TYPES. Holotype, male, Greenfield Mountain, Franklin Co., Massachusetts, 6 September 1925, G. C. Crampton. Two male and one female paratopotypes, 23 August to 6 September 1911, M. C. Van Duzee. Holotype and male paratopotypes are mounted on microscope slides. All types are in the collection of C. P. Alexander, NMNH. *Dicranoptycha microphallus* was described from a single specimen from Blood Mountain, Georgia, P. W. Fattig, 11

September 1945. The genitalia of the type are mounted on a microscope slide, the rest pinned. The type is in C. P. Alexander Collection, NMNH.

Taxonomic Characteristics. Basic coloration brownish gray. Male body length 6.5-7.5 mm, wing about 8.5 mm. Female body length 8.5-9 mm, wing 8.5-9 mm. *Head* yellowish gray with one row of dark bristles around each eye. Rostrum brown, palpi black. Antennae with scape, pedicel yellow, flagellomeres dark brown. Verticils long, about two and a half times length of their respective flagellomeres. *Thorax* with brown nota and pale yellow pleura. Pronotum and prescutum dark brown, with sparsely gray pruinosity, without longitudinal stripes. Pseudosutural foveae dark brown. Wings with faint brownish tinge, strongly iridescent under light at certain angles, costal fringe short in both sexes. Halteres brownish yellow. Legs with coxae and trochanters yellow, femora and tibiae light brown, tarsomeres brown. *Abdomen* with brown terga and brownish yellow sterna. In male, segments seven and eight form dark brown subterminal ring. Male hypopygium (Fig. 73) brownish yellow. Dorsal dististyle slender, apical half blackened and strongly denticulate on all surfaces. Ventral dististyle gradually narrowed to blunt tip. Male genitalia (Fig. 74) with vesica rounded. Lateral process slender, gradually tapered toward narrowly rounded, slightly turned upward and inward apex. Lateral apodeme broad in upper part. Anterior apodemes joined medially for most of their length, narrow basally and slightly bilobate, expanded and curved outward anteriorly. Ventral apodeme small, poorly defined. Aedeagus small, with small upcurved hook at posterior end. Aedeagal process with small, flat, plate-like upper part turned dorsad, and flattened, darkly sclerotized lower part, curved downward above aedeagus. Female genitalia (Fig. 75) of *germana* form. Cerci about same length as tenth segment, slender, curved upward to rounded tip. Hypovalves extending slightly beyond base of cerci, twelve setae on inner dorsal edge of each hypovalve. Posteroventral aspect of external reproductive structures as in Fig. 76.

Comparative Notes. D. septemtrionis most closely resembles *tennessa* in body coloration, but the small, inconspicuous aedeagus will readily separate males from *tennessa,* in which the aedeagus is large and massive. I have examined the type of *D. microphallus* which Alexander described from one male specimen. The genitalia were mounted at such an angle that the aedeagus was moved to one side and rotated so as to appear beside the aedeagal process with its side up. This might have led Alexander to regard *D. microphallus* as nearest to *septemtrionis* but with a slender aedeagus. Having compared several *D. septemtrionis* with the type of *microphallus,* I regard *microphallus* as a synonym of *septemtrionis.*

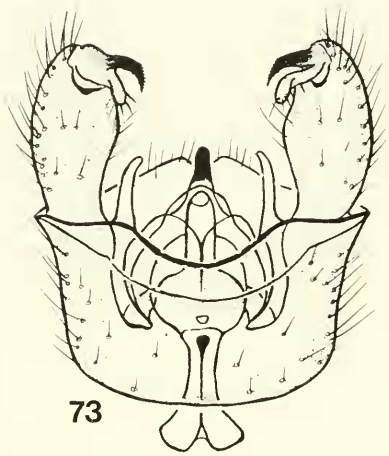
Geographic and Seasonal Distribution. The range of *D. septemtrionis* is from Massachusetts, New York, southern Michigan westward to eastern Kansas and southwestward to North Carolina and Georgia (Map 8). *D. septemtrionis* is the most common fall species of the genus in the eastern group. In eastern Kansas it can be found from late July to early September, with the peak of emergence in mid-August.

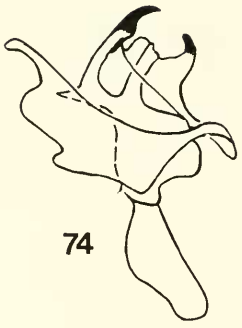
Summary of distribution: Georgia - Blood Mountain, 11 September. Indiana - Jefferson Co., 26 August. Kansas - Douglas Co., 16 July to 7 September. Kentucky - Grant Co., 6 August. Maryland - Prince Georges Co., 1 September; Plummers Island, 21 July. Massachusetts - Franklin Co., 23 August to 6 September. Michigan - Jackson Co., 9 August; Livingston Co., 9-28 August; Washtenaw Co., 13 August. New York - Niagara Co., 4 September. North Carolina - Avery Co., 4 September; Haywood Co., 4 September; Jackson Co., 29 August; Macon Co., 24 August to 4 September; Transylvania Co., 31 August; Yancey Co., 23 August. Ohio - Delaware Co., 4 September. Tennessee - Fentrees Co., 27 August. Virginia - Arlington, 20 August; Giles Co., 25 August to 5 September.

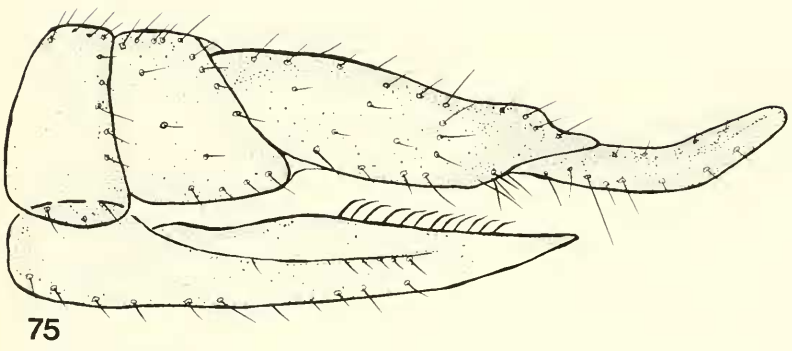
Dicranoptycha (Dicranoptycha) sobrina Osten Sacken

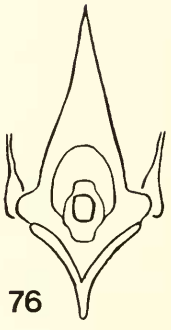
Dicranoptycha sobrina Osten Sacken, 1859, Proc. Acad. Nat. Sci. Philadelphia, 1850: 218.
Dicranoptycha sororcula Osten Sacken, 1859, Proc. Acad. Nat. Sci. Philadelphis, 1859: 218.
Dicranoptycha rogersi Alexander, 1927, Jour. N. Y. Entomol. Soc. 35: 55 (new synonymy).

Types. Osten Sacken originally described the species from seven males and five females col-

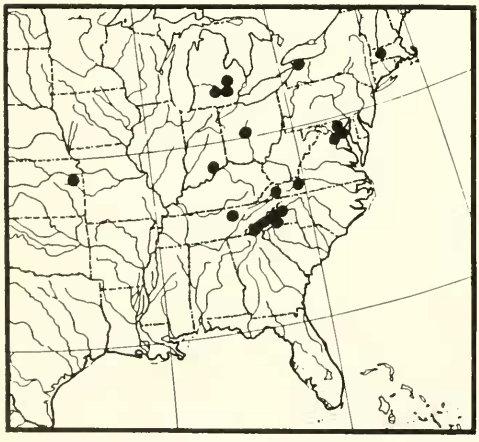








FIGURES 73-76. *Dicranoptycha (D.) septemtrionis*. 73, male hypopygium, dorsal aspect. 74, left lateral aspect with external skeleton removed. 75, female hypopygium, left lateral aspect. 76, postero-ventral aspect.



MAP 8. Known distribution of *Dicranoptycha septemtrionis*.

lected near Washington, D. C., in June 1859. Of these original twelve syntypes, one male and two females are in MCZ. The rest could not be found. *Dicranoptycha sororcula* was described from one male and one female from Dalton, Whitfield County, Georgia, July 1859. Osten Sacken placed this name in the synonymy of *D. sobrina* in 1869. I have been unable to locate the original specimens of *D. sororcula*. *Dicranoptycha rogersi* was described from seven specimens collected by J. S. Rogers in Marion County, Florida, on 13 April 1926. These specimens are in UMMZ.

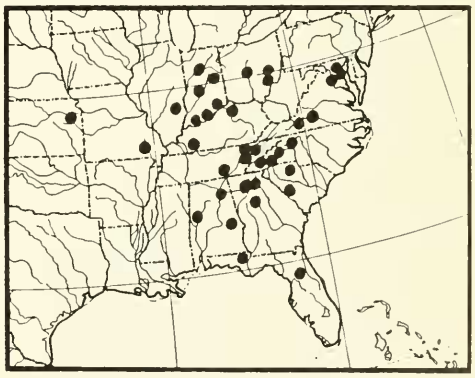
TAXONOMIC CHARACTERISTICS. Basic coloration grayish brown. Male body length 10-12 mm, wing 8-9 mm. Female body length 10-13 mm, wing 9-11 mm. *Head* gray, with single row of dark bristles around each eye. Rostrum and

palpi brown. Antennal flagellum brown, scape and pedicel paler. Verticils about three times as long as their respective flagellomeres. *Thorax* gray with yellowish brown pruinosity on all surfaces. Prescutum without longitudinal stripes. Pseudosutural foveae brown. Wings with pale cinereous tinge, costal margin darker; costal fringe dense and conspicuous, male with longer costal fringe than female. Halteres pale throughout. Legs mostly brownish yellow, fore femora dark brown, except basal one-fourth pale, remaining femora with brown tips. Tarsomeres dark brown except basal part of basitarsus paler. *Abdomen* with terga uniformly grayish brown; venter bicolorous, each sternum with anterior brown band and posterior yellow band. In male, segments six to eight blackened, forming darker, broad subterminal ring. Male hypopygium (Fig. 77) yellow. Dorsal dististyle broad at base, slightly curved, rather abruptly bent and acicular at apex, outer curvature denticulate, inner glabrous. Ventral dististyle shorter than dorsal one, evenly and slightly curved, apex blunt but not knobbed. Male genitalia (Fig. 78) with vesica oval. Lateral process extending to about two-thirds length of basistyle. Anterior apodemes broad, separated to base, widely divergent. Keel-like ventral apodeme well developed. Aedeagus large, darkened, curved upward from vesica, dorso-ventrally flattened with a dorsal, longitudinal depression, apex broadly rounded. Aedeagal process complicated, with upper, flattened, plate-like structure, darker at its posterior, broadly notched margin connected anteriorly to lower, upcurved, hook-like part situated medially in depression of aedeagus and attached to the base of aedeagus. Female genitalia (Fig. 79) of *germana* form. Cerci about same length as tenth segment, slightly narrowed and curved upward in apical half. Hypovalves extending to about midlength of cerci; eleven setae on inner dorsal edge of each hypovalve. Postero-ventral aspect of external reproductive structures as in Fig. 80, ninth sternum and genital furca fused together forming a ring-like structure.

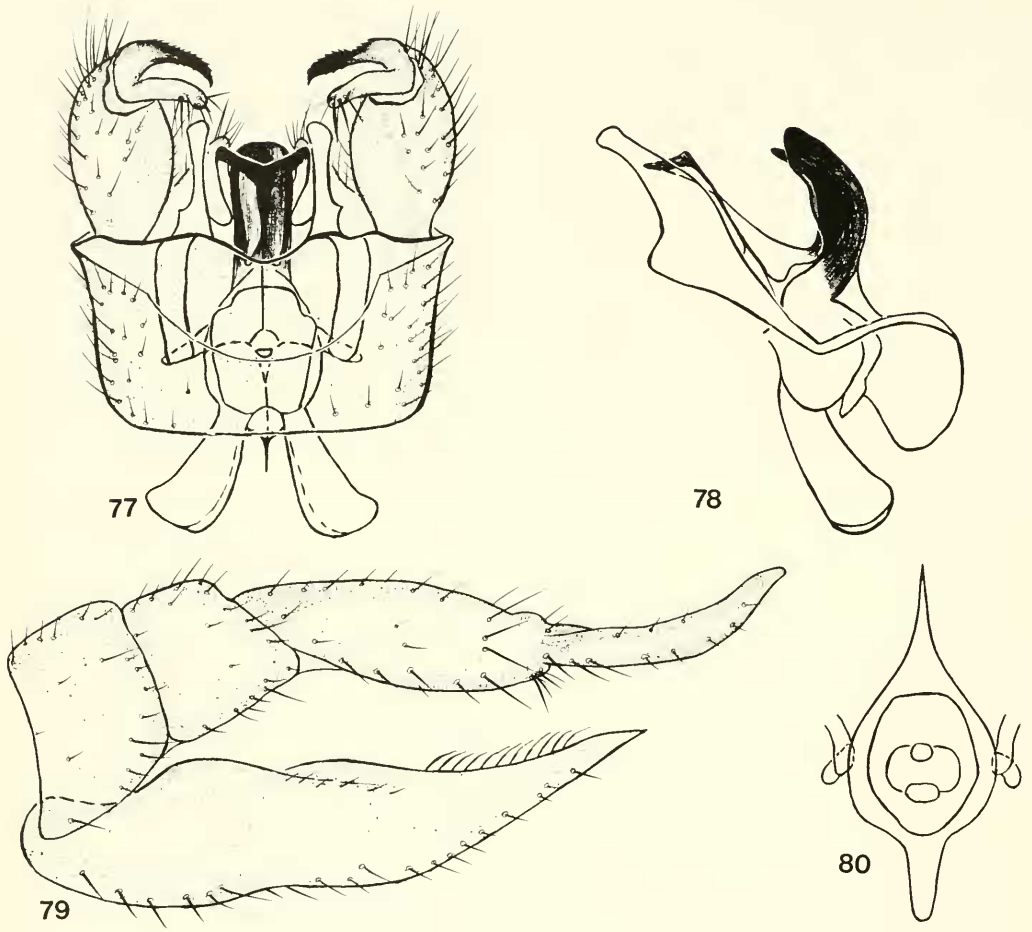
Comparative Notes. *D. sobrina* can be easily separated from other species except *nigripes* and *tigrina* by having banded abdominal sterna, but it differs from both those species in the location of the bands. In *D. sobrina* each sternum has an anterior dark transverse band while in *nigripes* and *tigrina* the dark band is at the middle of each sternum. *D. sobrina* can also often be recognized by its conspicuous dark brown fore femora, although this character is not constant. Most specimens are grayish brown with dark brown only on the fore femora. However, there is variation in over-all body coloration and the color of the femora. The specimens from Illinois, Kansas and Missouri, that is from the western part of the range, have yellowish brown body color and are uniformly light brown on all the femora. Members of the Florida population, which was described as *D. rogersi,* have an over-all dark brown body color and with dark brown on all the femora. Although the species varies in body color, banded abdominal sterna are persistent in all the populations. Having examined the type series of *D. rogersi* and specimens from other Floridian localities, I feel certain that *rogersi* is only an extreme color variant of *sobrina.*

Geographic and Seasonal Distribution. *D. sobrina* is the most widespread species of the genus. Its range extends from Maryland westward to eastern Kansas and southward through the Appalachian Mountains into central Florida (Map 9). *D. sobrina* has a late spring flight period in most of its range, except for the Florida population, where it was collected in late April and early May. In eastern Kansas, *D. sobrina* emerges in mid June and disappears by late June, while in most of the southeastern states occurrence of adults fly between late May and early June.

Summary of distribution: Alabama - Bibb Co., 25 May; De Kalb Co., 3 June;



MAP 9. Known distribution of *Dicranoptycha sobrina.*



FIGURES 77-80. *Dicranoptycha (D.) sobrina.* 77, male hypopygium, dorsal aspect. 78, left lateral aspect with external skeleton removed. 79, female hypopygium, left lateral aspect. 80, postero-ventral aspect.

Lee Co., 26 May. Florida - Jackson Co., 13 April to 9 May; Marion Co., 13 April. Georgia - Fulton Co., 1 June; Murray Co., 20 May; Whitfield Co., 27 May. Illinois - Effingham Co., 10 June. Indiana - Harrison Co., 13-18 June; Jefferson Co., 16 June; Marrion Co., 12 June; Owen Co., 24 June; Parke Co., 16 June; Spencer Co., 11 June. Kansas - Douglas Co., 15 June to 29 June. Kentucky - Christian Co., 3 June; Scott Co., 3 June. Maryland - Montgomery Co., 5 June; Prince Georges Co., 29 May to 1 June. Mississippi - Lee Co., 24 May. Missouri -Carter Co., 4 June. North Carolina - Buncombe Co., 29 May to 24 June; Jackson Co., 1 July; Transylvania Co., 5-10 June; Watauga Co., 22 June. Ohio - Athens Co., 12 June; Delaware Co., 15 June; Meigs Co., 4 June. South Carolina - Abbeville Co., 29 May; Spartanburg Co., 2 June. Tennessee - Fentress Co., 14-19 June; Grundy Co., 19 May; Morgan Co., 19 June; Scott Co., 29 May. Virginia - Floyd Co., 23 June; Giles Co., 18 June to 2 July; Prince William Co., 3 July.

Dicranoptycha (Dicranoptycha) spinifera, new species

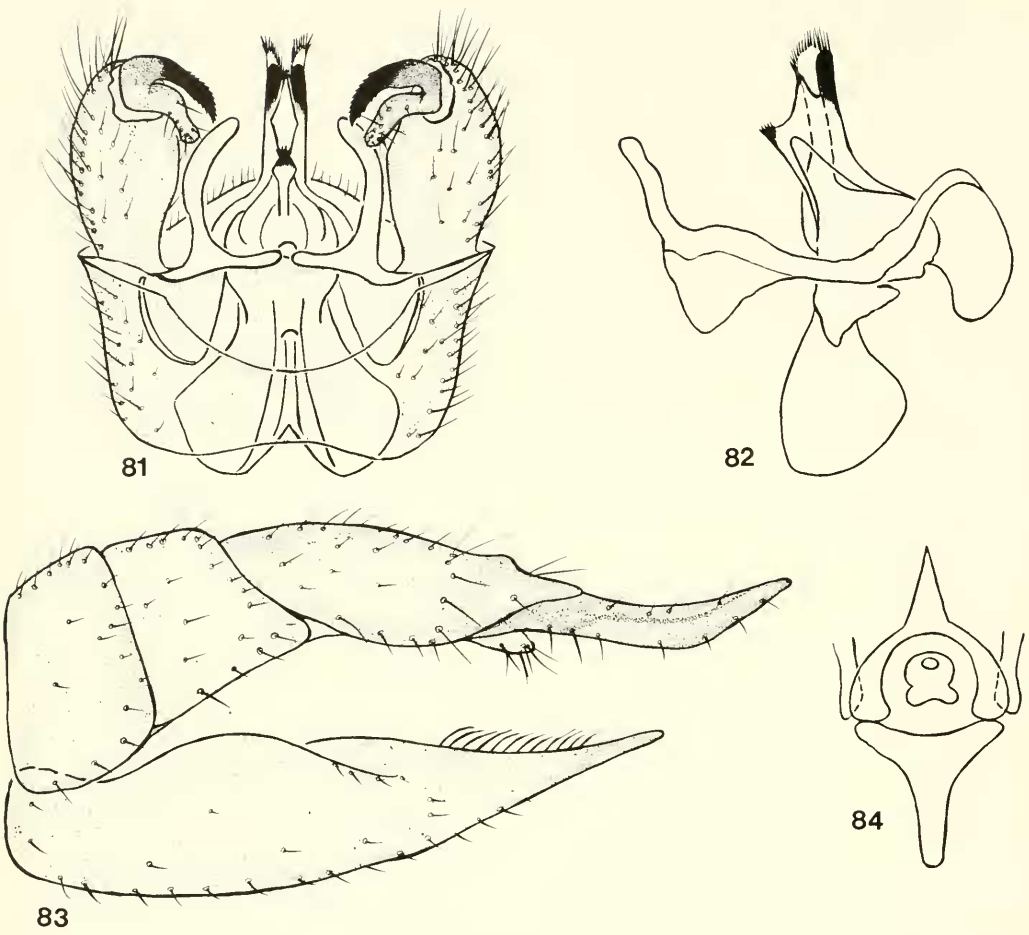
TYPES. Holotype, male, White Rock Ranch, White Rocks Forest Service Campground, near Kire, Giles County, Virginia, 3 June 1977, C.-W. Young 2. Allotype, taken in copulation with the holotype. Paratypes, 14 males and 8 females from vicinity of Mountain Lake Biological Sta-

tion, Giles County, Virginia, as follows: 24 June 1935, 1 male, 1 female; 25 June 1935, 2 females; 27 June 1935, 1 male; 28 June 1935, 1 female; all collected by R. E. Bellamy; 31 May 1946, 1 male; 4 June 1946, 2 males, 1 female; 6 June 1946, 3 males; 7 June 1946, 2 males, 1 female; 8 June 1946, 1 male, 1 female; 11 June 1946, 1 female; 25 June 1946, 1 male; all collected by J. S. Rogers; 23 June 1969, 1 male, collected by G. W. Byers; 3 June 1977, 1 male, collected by C.-W. Young. Specimens from elsewhere in the Appalachian region have not been included in the type series. The paratypes in the University of Michigan Museum of Zoology, collected by Bellamy and Rogers, had been determined by the latter as *D. acanthophallus.* Holotype, allotype and two male paratypes are in SEM. The rest of the paratypes are in UMMZ. The specific name refers to the spinose aedeagus of males.

Description. General coloration dark brown. Male body length 8.5-9 mm, wing 11 mm. Female body length 9.5-11 mm, wing 12 mm. *Head* gray, with one row of blackish bristles around each eye. Rostrum gray, palpi dark brown. Antennae with scape, pedicel and basal four flagellomeres yellow, outer flagellomeres brown. Scape oblong, twice as long as subspherical pedicel; flagellomeres longoval, their verticils conspicuous; first four flagellomeres each bearing 2 setae, fifth and subsequent each with four or five setae. *Thorax* mostly dark brown, with dense gray pollinosity, especially on pleura. Mesonotum dark gray, prescutum with indistinct median blackish gray stripe; pseudosutural foveae polished black. Wings smoky yellow with distinct brown seam along entire length of vein Cu. Veins testaceous, with setae on all longitudinal veins except 2A. Halteres pale throughout. Legs with coxae yellow. Trochanters yellow, femora and tibiae yellow to testaceous with brown tips. Basitarsi testaceous; tarsomeres dark brown. *Abdomen* dark brown, male hypopygium (Fig. 85) brown, dorsal dististyle arcuate, apical half blackened and strongly denticulate on all surfaces. Ventral dististyle broad at base, constricted before slightly dilated apex. Male genitalia (Fig. 86) with vesica oval, lateral processes conspicuous, extending to about three-fourths length of basistyle. Bases of lateral processes do not extend mesad and fuse to form dorsal bridge as in other species. Lateral apodeme broadly expanded in upper part. Anterior apodemes broad, fused medially along basal two-thirds of their length, apical one-third, forming two broad lobes. Ventral apodeme keel-like, well developed. Aedeagus conspicuous, elongate, with numerous distiinct spines at apex. Aedeagal process with narrowed, pointed upper part, dark, spiny, at posterior end connected beneath it a diamond-shaped lower part bent downward above aedeagus. Female genitalia (Fig. 87) of *germana* form; cerci about same length as tenth tergum, widest near mid-length, then evenly narrowed to apex; twelve setae on inner dorsal edge of each hypovalve. Postero-ventral aspect of external reproductive structures as in Fig. 88.

Comparative Notes. This species has been confused with *D. acanthophallus* because of the similarity in general appearance and because the original description of *acanthophallus* stated ". . . aedeagus stout and massive, near apex provided with more than a score of conspicuous erect spines." Alexander ordinarily described the terminal abdominal structures from slide-mounted specimens examined by compound microscope. Accordingly, the "conspicuous spines" on the aedeagus of *D. acanthophallus,* while distinct with such high magnification, are barely visible when viewed with a hand lens or stereoscopic dissecting microscope. *D. spinifera* can be easily separated from *acanthophallus* by visible spines at the tip of the aedeagus; by the narrowed, pointed upper part of the aedeagal process; and by its long and slender lateral process (Fig. 85) compared to that of *acanthophallus* (Fig. 37). *D. spinifera* also shows affinity with *byersi* in having a distinct brown seam along the entire length of vein Cu (see discussion under *byersi*). Females of these three species are less readily differentiated by external characters and can most reliably be separated by the structure of the ninth abdominal sternum and genital furca.

Geographic and Seasonal Distribution. *D. spinifera* is known from Pennsylvania to northern Georgia, where it is often found in the low Appalachian valleys (May 7). The types were collected in woods which included oaks, maple, yellow birch, hemlock, *Rhododendron,* tulip trees; understory of *Kalmia,* azaleas, abundant alder, locally deep growth of fern, skunk cabbage, and greenbriar. This is a late spring to early summer species. Rogers' collection from near Mountain Lake Biological Station,



FIGURES 81-84. *Dicranoptycha (D.) spinifera*. 81, male hypopygium, dorsal aspect. 82, left lateral aspect with external skeleton removed. 83, female hypopygium, left lateral aspect. 84, postero-ventral aspect.

Giles County, Virginia, indicates a flight period from late May to late June.

Summary of distribution: Georgia - Towns Co., 30 May; White Co., 1 June. North Carolina - Ashe Co., 27 June; Avery Co., 1 June; McDowell Co., 8 June; Watauga Co., 22 June; Yancey Co., 8 June. Pennsylvania - Lackawanna Co., 12 June. Tennessee - Sevier Co., 10 June. Virginia - Floyd Co., 23 June; Giles Co., 27 May to 27 June.

Dicranoptycha (Dicranoptycha) tennessa Alexander

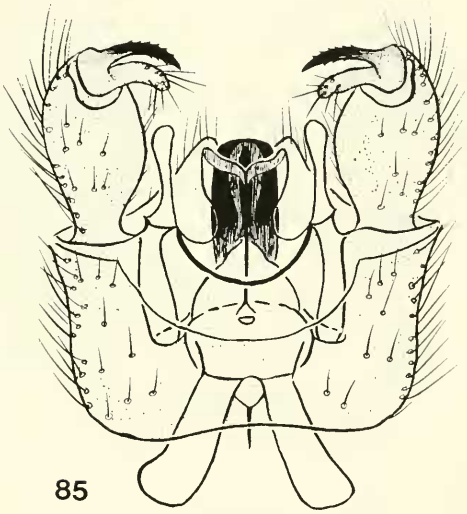
Dicranoptycha tennessa Alexander, 1941, Entomol. News. 52: 195.

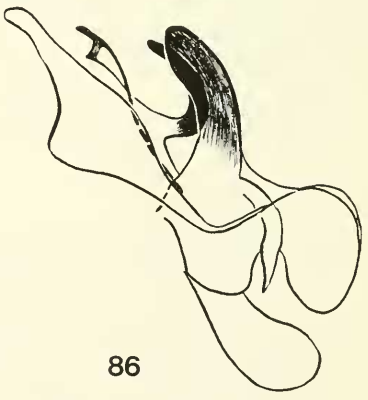
TYPES. Holotype, male, Knoxville, Knox County, Tennessee, 10 June 1939, A. C. Cole. Allotype, same data as holotype, and pinned with holotype. Both holotype and allotype are in the collection of C. P. Alexander, NMNH. The holotype is mounted on a microscope slide.

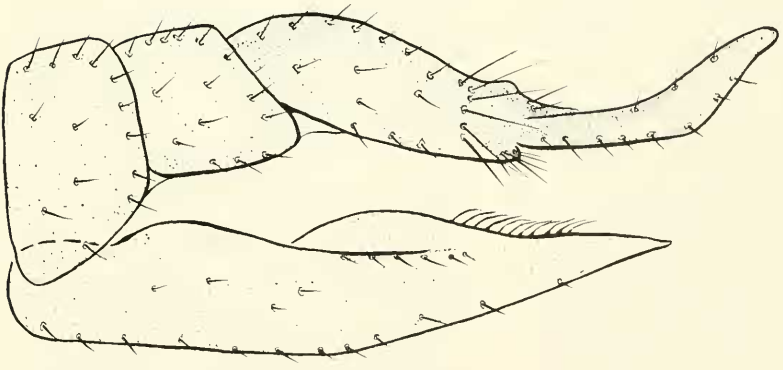
TAXONOMIC CHARACTERISTICS. General coloration grayish brown. Male body length 8-8.5 mm, wing 8.5 mm. Female body length about 9 mm, wing 9.5 mm. *Head* gray with one row of brown bristles around each eye. Rostrum dark brown, palpi brown. Antennae with yellowish scape and pedicel, flagellomeres brown. Verticils long, about three times length of their respective flagellomeres. *Thorax* with grayish brown nota and grayish pleura, densely pruinose on all surfaces. Prescutum without distinct longitudinal stripes.

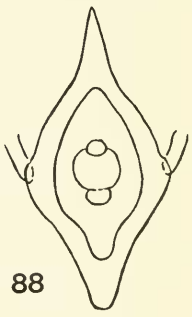
Pseudosutural foveae polished black. Wings with yellowish tinge, costal fringe long and conspicuous, 2A without setae. Legs with coxae testaceous yellow, trochanters obscure yellow. Remainder of legs light brown. *Abdomen* with terga brown, sterna brownish yellow. Male with darkened sixth, seventh and eighth segments and yellow hypopygium. Hypopygium (Fig. 85) with dorsal dististyle denticulate on outer two-thirds. Ventral dististyle evenly and slightly curved with blunt apex. Male genitalia (Fig. 86) with roughly oval vesica. Lateral process extending slightly beyond mid-length of basistyle. Lateral apodeme broad in upper part. Anterior apodemes separated at base, extending anteriorly into eighth segment. Ventral apodeme large, keel-like. Aedeagus of *sobrina* form, large, conspicuous, dorsoventrally flattened with broad, rounded apex. Aedeagal process with flattened upper part darkened at posterior margin, hook-like lower part bent downward then curved upward, attached to aedeagus at base. Female genitalia (Fig. 87) of *germana* form. Cerci slender at base, slightly broadened just beyond mid-length, then narrowed toward tips. Hypovalves extending slightly beyond mid-length of cerci, eleven setae on inner dorsal edge of each hypovalve. Postero-ventral aspect of female genitalia shows receptacle of aedeagal process beneath aperture of bursa copulatrix (Fig. 88).

Comparative Notes. D. tennessa has been misidentified as *sobrina* in some collections. Both species have long and conspicuous costal fringes and massive aedeagi. However, *D. tennessa* can be readily distinguished







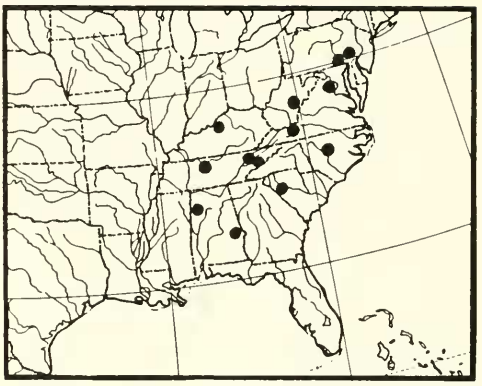


Figures 85-88. *Dicranoptycha (D.) tennessa.* 85, male hypopygium, dorsal aspect. 86, left lateral aspect with external skeleton removed. 87, female hypopygium, left lateral aspect. 88, postero-ventral aspect.

by its smaller body size and unbanded abdominal sterna. The similarity in male genitalia in these two species and *D. megaphallus* is discussed under *D. megaphallus*.

GEOGRAPHIC AND SEASONAL DISTRIBUTION. *D. tennessa* was previously known only from the type locality. The present study shows that *D. tennessa* has a wide range, from Pennsylvania southward to western Alabama (Map 10). It has a late May to mid June flight period in the southern part of its range and a mid June to early July one in the northern part.

Summary of distribution: Alabama - Hale Co., 26 May; Fayette Co., 24 May. Kentucky - Spencer Co., 6 June. North Carolina - Johnston Co., 28 May. Pennsylvania - Berks Co., 9 July; Lancaster Co., 12 July. South Carolina - Abbeville Co., 29 May. Tennessee - Knox Co., 10 June; Sevier Co., 13-17 June; Wilson Co., 4 June. Virginia - Giles Co., 26 June to 15 July; Prince William Co., 6 July. West Virginia - Greenbrier Co., 1 July.



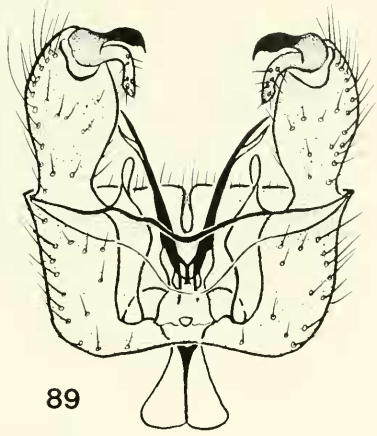
MAP 10. Known distribution of *Dicranoptycha tennessa*.

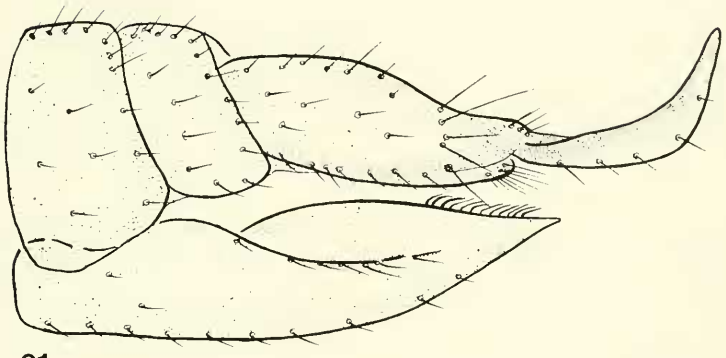
Dicranoptycha (Dicranoptycha) tigrina Alexander

Dicranoptycha tigrina Alexander, 1919, Entomol. News, 30: 21.

TYPES. Holotype, male, Lawrence, Douglas County, Kansas, altitude 900 feet, 16 July 1918, C. P. Alexander. Allotype, same data as holotype. Paratypes 50 males and females from 16 to 30 July 1918; no detailed data about the numbers of each sex were mentioned. Holotype, allotype and eight male and eleven female paratypes are in the collection of C. P. Alexander, NMNH. One male paratype is in the British Museum (Natural History), London. Two female paratypes are in SEM. One male and four female paratypes are in UMMZ. One male paratype is in CAS. The location of other paratypes is unknown. The holotype and three male paratypes are mounted on microscope slides.

TAXONOMIC CHARACTERISTICS. General coloration grayish brown. Male body length about 8 mm, wing 8.5 mm. Female body length 9 mm, wing 9 mm. *Head* dark brown, with one row of black bristles around each eye. Rostrum brownish yellow, palpi black. Antennae with yellow scape and pedicel, flagellomeres dark brown. Verticils short, slightly longer than their respective flagellomeres. *Thorax* grayish brown, prescutum brown with golden pruinosity, without longitudinal stripes, pleuron heavily covered with gray pruinosity. Pseudosutural foveae reddish brown. Wings with borwn tinge, highly iridescent under light at certain angles, costal fringe short. Legs with coxae brownish yellow, slightly pruinose at bases, trochanters and femora brownish yellow, tips of femora brown, tibiae and tarsomeres light brown. *Abdomen* with terga dark brown, the apical one-fifth of each segment more yellowish, sterna yellowish, segments three to seven with transverse blackened band near mid-length. Both terga and sterna producing a banded appearance. Male with darkened subterminal ring on seventh segment. Male hypopygium (Fig. 89) yellow. Dorsal dististyle constricted at about mid-length and arcuate to acute tip, both inner and outer curves glabrous. Ventral dististyle longer than dorsal one, strongly arcuate before mid-length. Male genitalia (Fig. 90) with small vesica. Lateral process short, extending slightly beyond one-fourth length of basistyle. Both upper and lower parts of lateral apodeme expanded. Anterior apodemes almost totally fused along mid-line, narrowed at base and expanded anteriorly, with slight notch at line of fusion. Ventral apodeme keel-like, well developed. Aedeagus inconspicuous both in dorsal and lateral aspects. Two long slender aedeagal processes arising from base of aedeagus, bent ventrad and branched near their tips. Female genitalia (Fig. 91) of *germana* form. Cerci slightly shorter than tenth tergum, narrowed at base, slightly broadened at mid-length and then narrowed toward upwardly curved tips. Hypovalvae reaching to about one-fourth length of cerci, twelve setae on inner dorsal edge of each hypovalve. Postero-ventral aspect of external reproductive structures as in Fig. 92, with long receptacles for branches of aedeagal process.





Figures 89-92. *Dicranoptycha (D.) tigrina.* 89, male hypopygium, dorsal aspect. 90, left lateral aspect with external skeleton removed. 91, female hypopygium, left lateral aspect. 92, postero-ventral aspect.

Comparative Notes. D. tigrina may be readily separated from the other two species with banded abdomen by having this striped, or tigrine appearance on both the terga and sterna of the abdomen. In the structure of the male genitalia, it is apparently close to *D. nigripes*. Differentiating the males of these two species is discussed under *D. nigripes*. Females of these two species can be separated by the structure of the receptacle for the aedeagal process, which in *D. tigrina* has a secondary branch near the tip (Fig. 92) and in *nigripes* near mid-length (Fig. 68).

Geographic and Seasonal Distribution. D. tigrina is known from Pennsylvania southward to North Carolina and southwestward to southern Oklahoma, widely spread from the Appalachian Mountains to the eastern plains and Ozark Mountain regions (May 6). In the discussion of *D. nigripes* I considered that *nigripes* and *tigrina* are closely related species that have excluded each other from their respective ranges. They both have about the same flight season, and examination from J. S. Rogers' extensive collections in Haywood County, North Carolina, and Giles County, Virginia, showed that all specimens collected were *D. tigrina*. It is a late summer, early fall species; in eastern Kansas it has a flight period from late August to mid September. It was often collected together with *D. septemtrionis*.

Summary of distribution: Arkansas - Polk Co., 30 July. Indiana - Jefferson Co., 27 August. Kansas - Douglas Co., 31 August to 20 September. Missouri -Miller Co., 23 August. North Carolina - Haywood Co., 27

July to 3 August. Oklahoma - Marshall Co., 2 July. Pennsylvania - Delaware Co., 25 August. Tennessee - Cumberland Co., 14 July. Virginia - Giles Co., 21-30 August.

Dicranoptycha (Dicranoptycha) winnemana Alexander

Dicranoptycha winnemana Alexander, 1916, Proc. Acad. Nat. Sci. Philadelphia, 1916: 500.

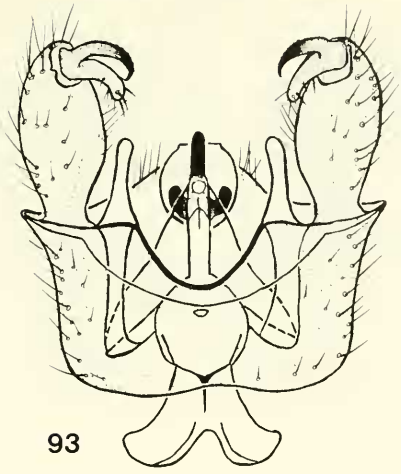
Types. Holotype, male, Plummers Island (or Winnemana, as the Indians called the island), Maryland, 21 July 1915, C. P. Alexander. Allotype, same data as holotype. Alexander (1916: 500) listed "paratopotypes, one male and ten females (McAtee and Alexander); paratype, one female, Dead Run, Virginia, July 21, 1915 (McAtee); one male, Lost Mountain, Cobb County, Georgia, July 13, 1913 (Bradley)." Holotype, allotype and most of the paratypes are in the collection of C. P. Alexander, NMNH. One female paratype is in CU (3483). The holotype and two male paratypes are mounted on microscope slides.

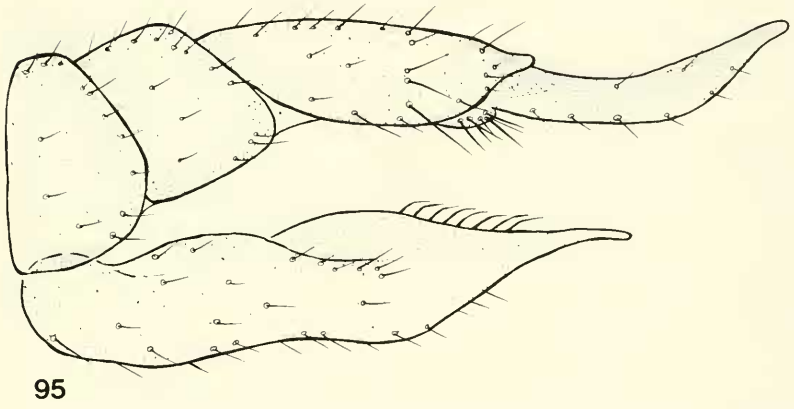
Taxonomic Characteristics. Basic coloration pale brownish yellow. Male body length 7-7.5 mm, wing 7.5 mm. Female body length 7.5-8.5 mm, wing 8-8.5 mm. *Head* ochraceous, with two rows of long bristles around each eye. Rostrum and palpi brown. Antennae with scape and pedicel dark brown, flagellomeres light brown. Verticils long, about twice length of their respective flagellomeres. *Thorax* pale brownish yellow with grayish pruinosity on pleura. Prescutum light brownish yellow, without stripes. Pseudosutural foveae dull yellow. Wings pale yellow, with setae on all longitudinal veins except 2A, costal fringes long and conspicuous, especially in males. Legs with coxae, trochanters, femora, tibiae and basitarsi yellow, outer four tarsomeres light brown. *Abdomen* brownish yellow. In male, seventh segment dark brown, forming subterminal ring, eighth segment and hypopygium brownish yellow. Male hypopygium (Fig. 93) with dorsal dististyle arcuate at apex, apex sharply pointed, outer curve slightly denticulate. Ventral dististyle larger than dorsal one, apex rounded but not enlarged. Male genitalia (Fig. 94) with vesica broadly oval. Lateral process with rounded apex, reaching to about mid-length of basistyle. Anterior apodemes well developed, fused for about half their length, broad at base, expanded and curved laterad anteriorly. Ventral apodeme small, keel-like. Both upper and lower parts of lateral apodeme equally expanded. Aedeagus short, with one short, darkened branch on each side. Aedeagal process with rod-like, darkly sclerotized upper part bent ventrad and connected anteriorly to enlarged lower part, which encloses aedeagus dorsally and laterally. Female genitalia (Fig. 95) of *germana* form. Cerci about same length as tenth segment, curved upward and narrowed at tips. Hypovalves with acuminate tips extending to about mid-length of cerci; eight setae on inner dorsal edge of each hypovalve. In postero-ventral aspect of external reproductive structures, receptacle of aedeagal process visible beneath and around sides of aperture of bursa copulatrix (Fig. 96).

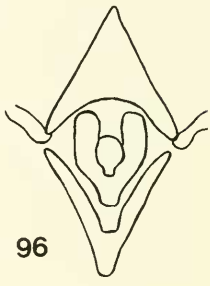
Comparative Notes. D. winnemana is the palest species in this genus in eastern North America. The only species with which it might be confused on the basis of color is *D. pallida.* For differentiation of these species see the discussion of the latter. Males of *D. winnemana* can be distinguished by the conspicuous genitalial characters, especially the enlarged lower part of the aedeagal process.

Geographic and Seasonal Distribution. D. winnemana is one of the more widespread species, its range approximating that of *sobrina. D. winnemana* occurs from Maryland to eastern Oklahoma and Texas and southward into western and central Florida (Map 11). It is a spring species. Its flight season starts in April in Florida and ends in July in northern parts of the range. About 8:15 on the morning of 24 May 1978, about 20 mating pairs were collected at Tombigbee State Park, Lee County, Mississippi. They were found mostly in mixed woods—white oak, hickory, tulip tree, and ash, with some dogwood, sassafras, and mulberry; undergrowth of poison ivy, wild grape, wild rose, Virginia creeper, and green brier. Mating pairs were found about two feet above the ground on undergrowth leaves.

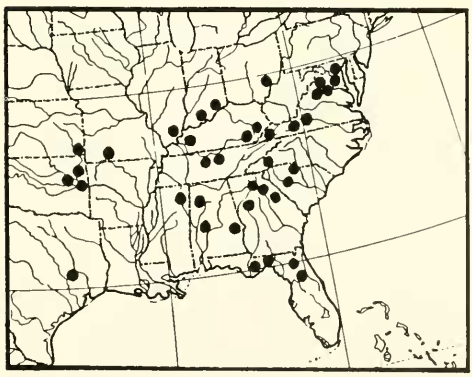
Summary of distribution: Alabama - Fayette Co., 24 May; Hale Co., 25 May; Lee Co., 26 May. Florida - Alachua Co., 26-30 May; Jefferson Co., 27 April; Leon Co., 16 April; Marion Co., 11 May. Georgia - Clarke Co., 29 May; Cobb Co., 13 June; Dawson Co., 22 June; Hall Co., 6 June. Illinois - Pope Co., 14 July. Indiana - Floyd Co., 17 July; Jefferson Co., 7 July. Kansas - Cherokee Co., 24 June. Kentucky -







FIGURES 93-96. *Dicranoptycha (D.) winnemana.* 93, male hypopygium, dorsal aspect. 94, left lateral aspect with external skeleton removed. 95, female hypopygium, left lateral aspect. 96, postero-ventral aspect.



MAP 11. Known distribution of *Dicranoptycha winnemana.*

Bell Co., 18 June; Christian Co., 12 June; Whitley Co., 24 June. Maryland - Montgomery Co., 30 June. Mississippi - Lee Co., 24 May. Missouri - Taney Co., 12 June. North Carolina - Haywood Co., 20 June. Ohio - Athens Co., 21 July. Oklahoma - Adair Co., 17 June; Delaware Co., 10 June; Le Flore Co., 23 June; Rogers Co., 19 June. South Carolina - Abbeville Co., 30 May; Spartanburg Co., 2-5 June. Tennessee - Fentress co., 28 June; Wilson Co., 20 June. Texas -Brazos Co., 10 May. Virginia - Fairfax Co., 23 July; Giles Co., 9-15 July; Greene Co., 14 July; Montgomery Co., 15 July; Rappahannock Co., 30 June; Shenandoah Co., 5 July; Washington Co., 30 June.

THE *MELAMPYGIA* GROUP

Dicranoptycha (Dicranoptycha) melampygia Alexander

Dicranoptycha melampygia Alexander, 1950, Pan-Pacific Ent. 26: 81.

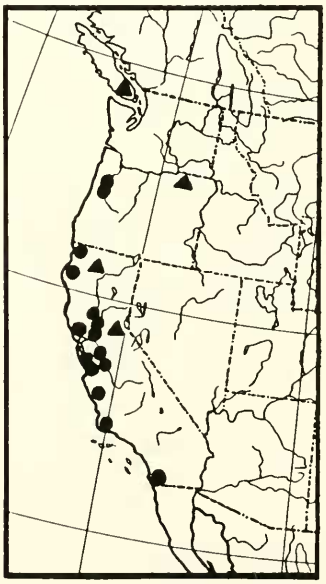
TYPES. Holotype, male, Prairie Creek State Park, Humboldt County, California, 11 August 1948, C. P. Alexander. Three male and one female paratypes, Peavine Ridge, Yamhill Co., Oregon, 12 July 1945, K. M. Fender; one male paratype from Zena, Eola Hills, Polk County, Oregon, 5 June 1940, K. M. Fender. All types are in the collection of C. P. Alexander, NMNH. The holotype and three male paratypes are mounted on microscope slides.

TAXONOMIC CHARACTERISTICS. General coloration brown. Male body length 8.5-9 mm, wing 8-9 mm. Female body length 9-9.5 mm, wing 9.5 mm. *Head* dark gray, with one row of brown bristles around each eye. Rostrum brown, palpi dark brown. Antennae with scape and pedicel obscure yellow, flagellomeres dark brown. Verticils about one and a half times the length of their respective flagellomeres. *Thorax* brown, with golden pruinosity on nota and gray pruinosity on pleura. Prescutum without longitudinal stripe. Pseudosutural foveae brown. Wings with brown tinge, costal fringe short and dense. Legs with coxae brown, pruinose, trochanters and femora obscure yellow, tibiae and tarsi brown. *Abdomen* dark brown, without subterminal ring. Male hypopygium (Fig. 97) with dorsal dististyle evenly curved, gradually narrowed to slender apical spine, outer curvature denticulate. Ventral dististyle broad at base, narrowed near mid-length, with obtusely rounded apex. Male genitalia (Fig. 98) with small vesica. Lateral process reaching to about mid-length of basistyle, with flange on outer apical margin of acute, outwardly curved tip. Both upper and lower parts of lateral apodemes expanded. Anterior apodemes fused medially for most of their length with dorsal crest formed along line of fusion, their combined bases about same width as vesicle, widened and rounded anteriorly, with slight median notch. Ventral apodeme small, aedeagus short. Aedeagal process flat, platelike, connected medially to top of aedeagus. Female genitalia (Fig. 99) with cerci short, broad, spatulate, shorter than tenth tergum. Very long hairs around posterior end of tenth tergum and on margin of slightly expanded cercal base. Hypovalves extending to about base of cerci, eleven setae on inner dorsal edge of each hypovalve. Postero-ventral aspect of external reproductive structures, as in Fig. 100, ninth sternum and genital furca fused together.

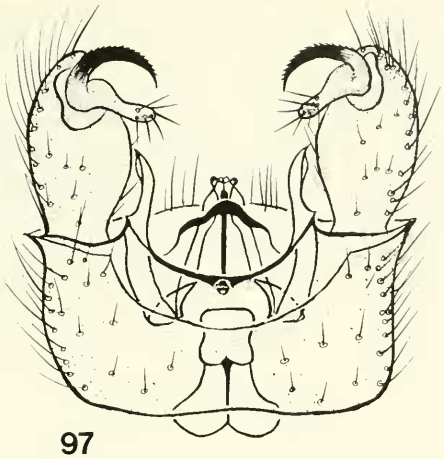
COMPARATIVE NOTES. This species and *D. occidentalis* are closely related. However, *D. melampygia* may be distinguished from *occidentalis* by the dark brown body color, dense costal fringe, and detailed structure of the male genitalia. The similarity between *D. melampygia* and *nigrogenualis* is covered in the discussion of the latter.

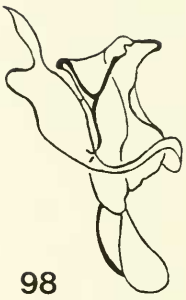
GEOGRAPHIC AND SEASONAL DISTRIBUTION. *D. melampygia* is known from the Coast Ranges from southern California to northern Oregon (Map 12). Its range overlaps that of *D. occidentalis* in California, but intermediate specimens are unknown. Specimens have been collected from early April to mid July. All April records are from low altitudes in southern California.

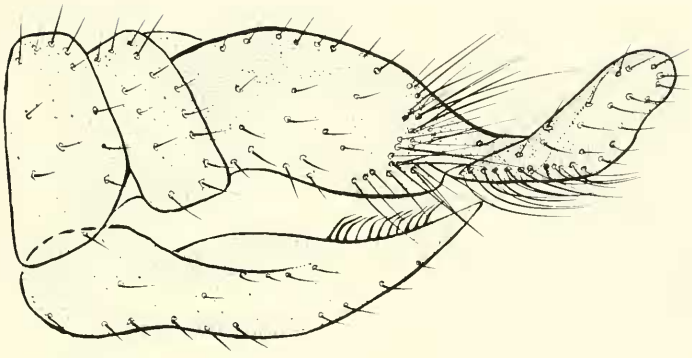
Summary of distribution: California - Alameda Co., 4-14 May; Contra Costa Co., 13 May; Del Norte Co., 19-22 June; Humboldt Co., 27 May; Marin Co., 13-25 May, 1 June; Monterey Co., 8 May to 1 June; Napa Co., 9 May; San Diego Co., 10-21 April; San Mateo Co., 16 May; Santa Barbara Co., 18-21 May; Santa Clara Co.,

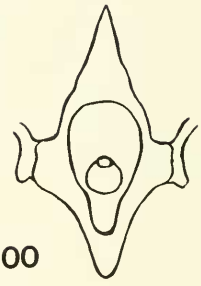


MAP 12. Known distribution of *Dicranoptycha melampygia* (circles) and *D. spinosissima* (triangles).









Figures 97-100. *Dicranoptycha (D.) melampygia.* 97, male hypopygium, dorsal aspect. 98, left lateral aspect with external skeleton removed. 99, female hypopygium, left lateral aspect. 100, postero-ventral aspect.

3 June; Santa Cruz Co., 2 June; Sonoma Co., 8 May. Oregon - Polk Co., 5 June, Yamhill Co., 12 July.

Dicranoptycha (Dicranoptycha) nigrogenualis Alexander

Dicranoptycha nigrogenualis Alexander, 1949, Amer. Midland Nat., 42: 291.

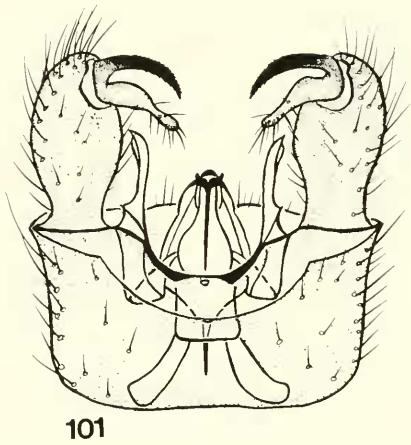
Types. Holotype male, Boulder Lake trail from Olympic Hot Springs, Olympic National Park, altitude 3,400 ft., Clallam County, Washington, 5 August 1947, M. M. Alexander. Allotype, Sahale Falls, Mount Hood, altitude 4575 ft., Hood River County, Oregon, 17 July 1947, C. P. Alexander. Types are slide-mounted and are in the collection of C. P. Alexander, NMNH.

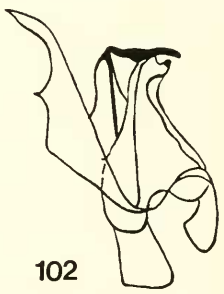
Taxonomic Characteristics. General coloration dark brown. Male body length about 11 mm, wing 11 mm. Female body length 11.5 mm, wing 11 mm. *Head* dark gray, with one row of dark bristles around each eye. Rostrum and palpi dark brown. Antennae with scape brown, pedicel obscure yellow, flagellomeres brown. Verticils about one and a half times length of their respective flagellomeres. *Thorax* with prescutum dark brown, without longitudinal stripes, pleura uniformly reddish brown with gray pruinosity. Pseudosutural foveae polished black. Wings brownish yellow, costal margin darker with short fringe, vein 2A without setae. Legs with coxae, trochanters yellow, femora yellow, apical one-fourth conspicuously blackened, tibiae brownish yellow, basitarsi light brown, outer tarsomeres dark brown. *Abdomen*

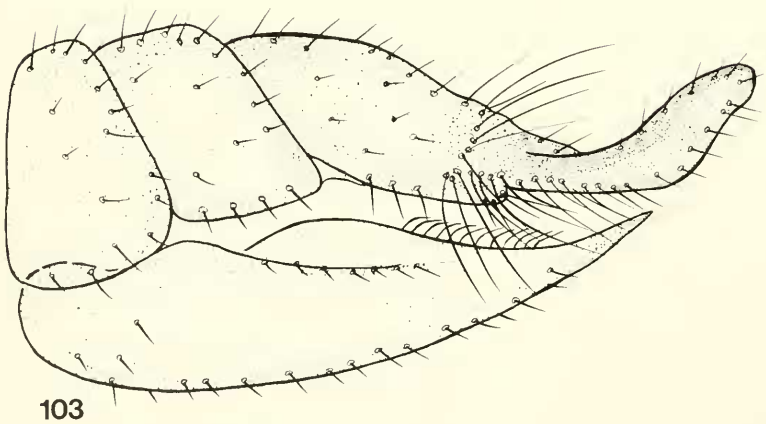
black, sparsely pruinose hypopygium. Male hypopygium (Fig. 101) brown with dorsal dististyle long, slender, narrowed toward tip denticulate on distal two-thirds. Ventral dististyle with basal half stout, outer half narrowed to rounded apex. Male genitalia (Fig. 102) with lateral process slender, with spine-like tip directed laterad, outer margin with low flange. Lateral apodeme slightly expanded in upper part. Anterior apodemes widely separated at base, diverging from anterior corners of somewhat quadrate vesica. Ventral apodeme keel-like, well developed, slightly smaller than anterior apodeme. Aedeagus short, inconspicuous, with two tiny, sclerotized lobes at lower end. Aedeagal process with flat, plate-like upper part (phallosome, Alexander 1949), darker at posterior margin connected posteriorly to bar-like lower part hanging down behind aedeagus.

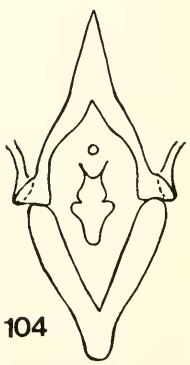
Female genitalia (Fig. 103) of *melampygia* form. Cerci slightly shorter than tenth segment, narrowed at base and broadly expanded beyond mid-length, with blunt tips. A circle of long setae near posterior end of the tenth segment. Hypovalves sharp-tipped, reaching approximately to mid-length of cerci. Twelve setae on inner dorsal edge of each hypovalve. Postero-ventral aspect of external reproductive structure shows slightly sclerotized receptacle for aedeagal process below aperture of bursa copulatrix (Fig. 104).

COMPARATIVE NOTES. D. nigrogenualis is differentiated from *stenophallus* and *spinosissima* by its larger body size, by its overall darker color, and by having a flange on the outer margin of the lateral process. Although the widely spaced anterior apodemes separate









FIGURES 101-104. *Dicranoptycha (D.) nigrogenualis.* 101, male hypopygium, dorsal aspect. 102, left lateral aspect with external skeleton removed. 103, female hypopygium, left lateral aspect. 104, postero-ventral aspect.

males of this species from all other western species, they are not visible except in specimens that have been cleared.

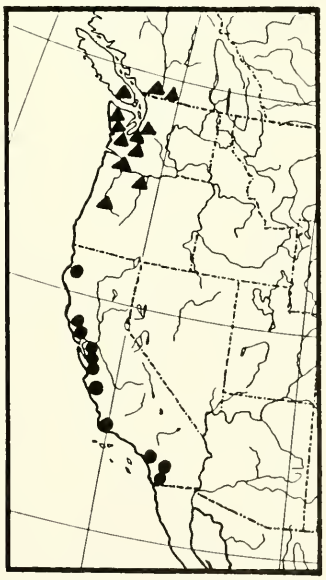
Geographic and Seasonal Distribution. *D. nigrogenualis* has been recorded from southern British Columbia to Oregon, mainly in the Coast Ranges (Map 13). Examination of a series of specimens of this species (UMMZ) shows it has a mid-summer flight season.

Summary of distribution: British Columbia - Abbotsford, 27 June; Vancouver, 21 July; Vancouver Island, 31 July to 13 August. Oregon - Benton Co., 26 July; Hood River Co., 28 June. Washington - Clallam Co., 5 August; Cowlitz Co., 17 July; Grays Harbor Co., 12 July; Jefferson Co., 27 July; King Co., 19 July; Lewis Co., 2-12 July; Thurston Co., 28 July.

Dicranoptycha (Dicranoptycha) occidentalis Alexander

Dicranoptycha occidentalis Alexander, 1927, Proc. U. S. Natl. Mus., 72(2): 10.

Types. Holotype, male, Alpine, San Diego County, California, 10 April 1915, M. C. Van Duzee. Paratypes, two broken males, one from Muir Woods, Marin County, California, 19 May 1915, the other from Berkeley, Alameda County, California, 14 May 1915, both collected by M. C. Van Duzee. The holotype and paratypes are all mounted on microscope slides in the collection of C. P. Alexander, NMNH.

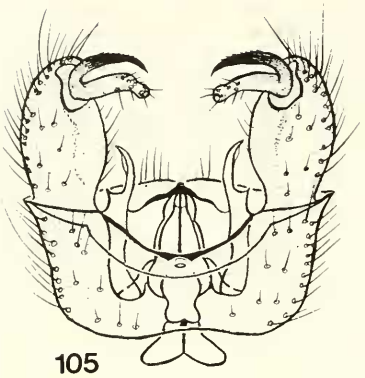


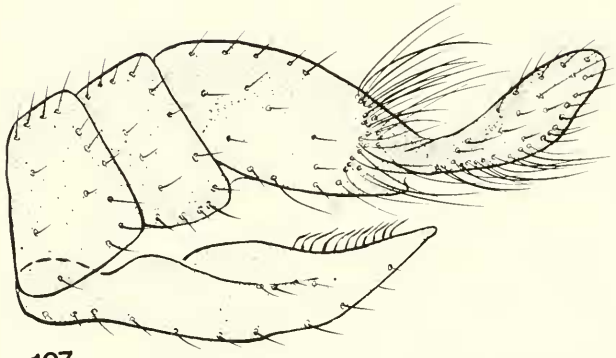
MAP 13. Known distribution of *Dicranoptycha nigrogenualis* (triangles) and *D. occidentalis* (circles).

Taxonomic Characteristics. Basic coloration grayish yellow. Male body length 7.5-8 mm, wing 8.5 mm. Female body length 8.5-9 mm, wing 9 mm. *Head* ashy gray, with one row of brown bristles around each eye. Rostrum light brown, palpi dark brown. Antennae with scape and pedicel yellow, flagellomeres brown, verticils about same length as their respective flagellomeres. *Thorax* brownish yellow, prescutum with an obscure brown median line. Pseudosutural foveae indistinct. Wings with yellowish tinge, highly iridescent under light at certain angles, costal fringe short, 2A without setae. Legs and basitarsi yellow, four outer tarsomeres brown. *Abdomen* yellowish brown. In male, segments seven and eight forming darkened subterminal ring. Male hypopygium (Fig. 105) with dorsal dististyle slender, evenly curved to terminal spine, outer curvature denticulate. Ventral dististyle slightly larger than dorsal one, tapering slightly from base to rounded apex. Male genitalia (Fig. 106) with small vesica. Lateral process with flange on outer apical margin and acute tip curved laterad. Lateral apodeme broad in upper part. Anterior apodemes narrow at base, widened anteriorly, fused for more than half their length with crest along median line. Ventral apodeme small, poorly defined. Aedeagus blunt, without any projection. Aedeagal process flat, plate-like, connected medially to top of aedeagus. Female genitalia (Fig. 107) of *melampygia* form. Cerci shorter than tenth segment, long hairs along basal ventral margin and near posterior end of tenth segment. Hypovalve reaching approximately to base of cerci, eleven setae on inner dorsal edge of each hypovalve. Postero-ventral aspect of external reproductive structures as in Fig. 108.

Comparative Notes. Specimens of this species and of *D. stenophallus* closely resemble each other externally. The specific characters that distinguish these species are covered in the discussion of the latter. The grayish yellow body color and the darkened subterminal ring separate males of *D. occidentalis* from those of *melampygia,* the only species with which it may be confused on the structure of male genitalia.

Geographic and Seasonal Distribution.





FIGURES 105-108. *Dicranoptycha (D.) occidentalis*. 105, male hypopygium, dorsal aspect. 106, left lateral aspect with external skeleton removed. 107, female hypopygium, left lateral aspect. 108, postero-ventral aspect.

D. occidentalis is known only from California, along the Coast Ranges (Map 13). This species is closely related to *D. melampygia*. Specimens have been collected in habitats drier than that of *D. melampygia*, such as chaparral. The flight season starts in April in southern California and lasts into July in northern California.

Summary of distribution: California - Alameda Co., 21 June; Humboldt Co., 30 July; Los Angeles Co., 19 May, Marin Co., 19 May; Monterey Co., 1-20 June; Riverside Co., 29 April to 29 May; San Diego Co., 10 April; Santa Barbara Co., 18-21 May; Santa Clara Co., 29 April; Santa Cruz Co., 2 June; Sonoma Co., 8-17 July.

Dicranoptycha (Dicranoptycha) quadrivittata Alexander

Dicranoptycha sobrina quadrivittata Alexander, 1919, Canad. Entomol. 51: 191.

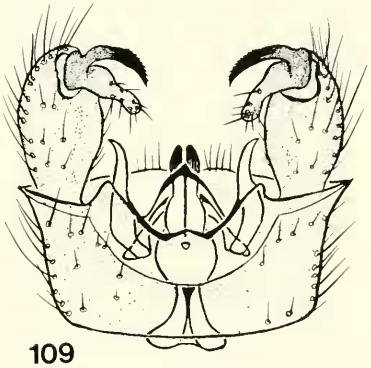
Dicranoptycha quadrivittata Alexander, 1927, Proc. U. S. Natl. Mus. 72(2): 10.

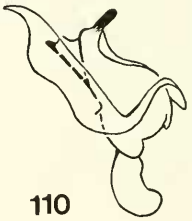
TYPES. Holotype, female, Peaceful Valley, Boulder County, Colorado, 25 August 1917, T. D. A. Cockerell. The holotype is in the collection of C. P. Alexander, NMNH.

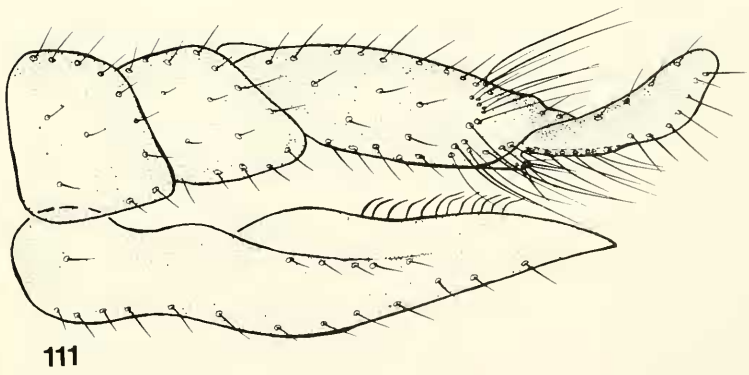
TAXONOMIC CHARACTERISTICS. Basic coloration gray. Male body length 8.5-9 mm, wing 9 mm. Female body length 9.5 mm, wing 10 mm. *Head* ashy gray, with one row of brown bristles around each eye. Rostrum grayish brown, palpi dark brown. Antennae with yellow scape and pedicel, flagellomeres dark brown. Verticils short, about same length as their respective flagellomeres. *Thorax* gray, with pruinosity on all surfaces. Prescutum gray, with four longitudinal stripes, median pair longest, dark brown, parallel and separated from each other by gray line, lateral stripes short, indistinct. Pseudosutural foveae reddish brown. Wings with tawny tinge, vein 2A without setae, costal fringe short. Legs with coxae gray, slightly pruinose,

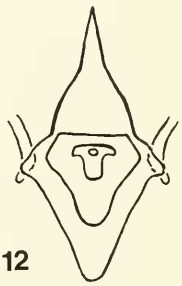
femora, tibiae and most of tarsi testaceous, apical tarsomeres brown. *Abdomen* with terga brown, sterna brownish yellow. Male with segments seven and eight dark brown, forming broad subterminal ring. Male hypopygium (Fig. 109) brown. Dorsal dististyle evenly curved to sharp apex, outer curvature denticulate. Ventral dististyle broad at base, abruptly narrowed at mid-length, apex rounded. Male genitalia (Fig. 110) with small vesica. Lateral process with pointed apex, curved laterad reaching to about mid-length of basistyle. Anterior apodemes small, about same size as vesica, fused medially, narrow at base, with slight indentation between them at anterior margin. Lateral apodeme narrow in lower part, upper part slightly expanded. Ventral apodeme small, keel-like. Aedeagus small, short, with two finger-like projections at its posterior end bent ventrad. Aedeagal process flattened, sinuate at sides and narrowed toward darker, pointed posterior margin, connected medially to top of aedeagus. Female genitalia (Fig. 111) of *melampygia* form. Cerci shorter than tenth segment, narrowed at base and expanded broadly near mid-length narrowing slightly toward rounded apex. Long setae around posterior end of tenth tergum and along margins of expanded cercal bases. Hypovalves reaching to about mid-length of cerci; twelve setae on inner dorsal edge of each hypovalve. Postero-ventral aspect of external reproductive structures as in Fig. 112, ninth sternum and genital furca fused together.

COMPARATIVE NOTES. The distinct grayish color of *D. quadrivittata* makes it distinguishable from all of the other western species of the genus. The similarly grayish eastern species, *D. tennessa,* can be separated by the genitalial structures of both sexes. The latter has a large, distinct aedeagus in the male and its female has slender, longer, more acute cerci. Having examined the holotype female and several specimens from areas other than the type locality, I agree with Dr. Alexander that *D. quadrivittata* deserves full species status. The







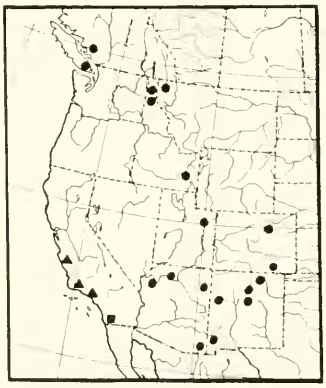


FIGURES 109-112. *Dicranoptycha (D.) quadrivittata.* 109, male hypopygium, dorsal aspect. 110, left lateral aspect with external skeleton removed. 111, female hypopygium, left lateral aspect. 112, postero-ventral aspect.

cerci of the female holotype are quite different from those of *D. sobrina*. The shape of the cerci suggest a close relationship of this species to the western species group rather than to the eastern one. This is also true for the male genitalic structures, in which *D. quadrivittata* most closely resemble *melampygia* and *occidentalis* in having a small aedeagus and aedeagal process. It differs from these two species most noticeably by having two finger-like projections at the posterior end of the aedeagus.

GEOGRAPHIC AND SEASONAL DISTRIBUTION. *D. quadrivittata* is the most widespread species in the western species group; it ranges from southern British Columbia southeastward to southern Arizona and central Colorado (Map 14). It is the only species that inhabits the Rocky Mountains and associated ranges. It is unknown from the Pacific Coast States, but overlaps the range of some other western species in southern British Columbia. It is a summer species, collected during June, July and August.

Summary of distribution: Arizona - Apache Co., 25 June; Cochise Co., 8 July; Coconino Co., 7 July; Mohave Co., 18 July. British Columbia - Squamish, 5 August; Terrace, 4-7 August (not shown on map); Vancouver Island, 17 August. Colorado - Boulder Co., 25 August; Las Animas Co., 27 July. Idaho - Bingham Co., 27 July; Bonner Co., 3 July; Kootenai Co., 1 July. Montana - Lincoln Co., 31 July. New Mexico - Colfax Co., 27 June; Grant Co., 31 July; Santa Fe Co., 6 August; Torrance Co., 25 July; Valencia Co., 9 August. Utah - Duchesne Co., 1 July.



MAP 14. Known distribution of *Dicranoptycha quadrivittata* (circles), *D. linsdalei* (triangles) and *D. laevis* (square).

Dicranoptycha (Dicranoptycha) spinosissima Alexander

Dicranoptycha spinosissima Alexander, 1950, Pan-Pacific Entomol. 26: 83.

TYPES. Holotype, male, Hatchet Pass near Burney, Shasta County, California, 9 July 1947, C. P. Alexander. Allotype, Little Phillips Creek above Elgin, Blue Mountains, Umatilla County, Oregon, 2 July 1948, C. P. Alexander. One male paratype same data as allotype. All types are in the collection of C. P. Alexander, NMNH. The holotype and paratype are mounted on microscope slides.

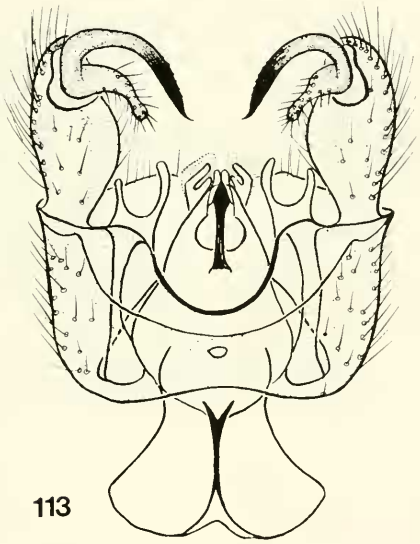
TAXONOMIC CHARACTERISTICS. Basic coloration grayish brown. Male body length 9-10 mm, wing 9.5 mm. Female body length 10 mm, wing 10.5 mm. *Head* gray, with one row of dark brown bristles around each eye. Rostrum brown, palpi black. Antennae with scape and pedicel yellow, flagellomeres black. Verticils about one and a half times length of their respective flagellomeres. *Thorax* mostly grayish brown with strong pruinosity on all surfaces. Prescutum darker with two pale faint longitudinal stripes. Pseudosutural foveae dark brown. Wings with brown tinge, strongly iridescent under light at certain angles, costal fringe short, vein 2A without setae. Legs with coxae brownish yellow, remainder of legs yellow, three outer tarsomeres brown. *Abdomen* brown. In male, posterior half of segment six and entire seventh and eighth segments forming broad, darkened subterminal ring. Male hypopygium (Fig. 113) brownish yellow. Dorsal dististyle long, slender, evenly curved, gradually narrowed to sharp apical spine; outer curvature denticulate on apical one-third. Ventral dististyle short, broad at base, narrowed at mid-length. Male genitalia (Fig. 114) with large, roughly oval vesica. Lateral process short, two-branched, extending to about one-third length of basistyle. Lateral apodeme with expanded lower part. Anterior apodemes nearly completely fused along mid-line to form single large structure about same size as vesica, broadly connected with vesica at base, slightly notched anteriorly with high median crest, greatest width about twice width at base. Ventral apodeme small, slender, keel-like. Aedeagus short, broad, with two small lobes on dorsal posterior margin; ventral posterior end produced on each side into two slender rods extending dorsad and covered by pale membrane densely set with small setae. Aedeagal

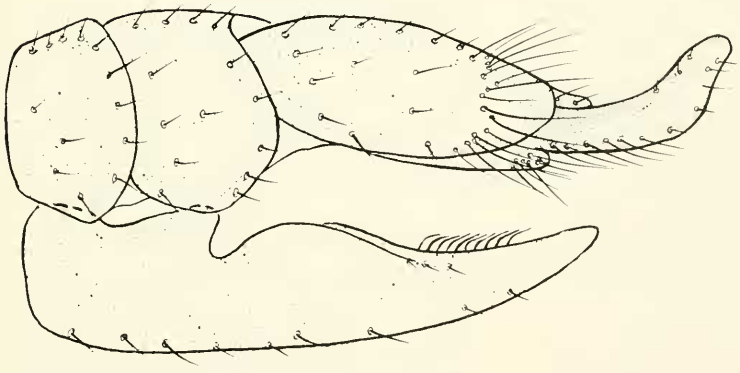
process lance-shaped, connected medially to top of aedeagus. Female genitalia (FIg. 115) of *melampygia* form. Cerci shorter than tenth segment, broad, slightly expanded near mid-length. Hypovalves reaching to about one-third length of cerci, ten setae on dorsal inner edge of each hypovalve. In postero-ventral aspect of external reproductive structures, ninth sternum and genital furca separated, receptacle for aedeagal process absent (Fig. 116).

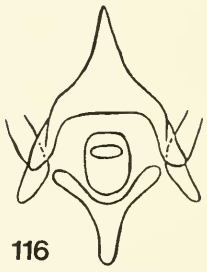
Comparative Notes. The long, slender dorsal dististyle, the two branched lateral process and the distinct spiny membrane around the apex of the aedeagus will at once separate males of *D. spinosissima* from those of all other species in the genus.

Geographic and Seasonal Distribution. *D. spinosissima* is known from southwestern British Columbia to northern California, including the northern Coast Ranges, Blue Mountains, Cascade Range and northern Sierra Nevada, but it has not been recorded from the Coast Ranges of California (Map 12). This species emerges in June and July in California and August in British Columbia.

Summary of distribution: British Colum-







Figures 113-116. *Dicranoptycha (D.) spinosissima.* 113, male hypopygium, dorsal aspect. 114, left lateral aspect with external skeleton removed. 115, female hypopygium, left lateral aspect. 116, postero-ventral aspect.

bia - Vancouver Island, 9-16 August. California - El Dorado Co., 6 June; Shasta Co., 7-9 July. Oregon - Umatilla Co., 2 July.

Dicranoptycha (Dicranoptycha) stenophallus Alexander

Dicranoptycha stenophallus Alexander, 1950, Pan-Pacific Ent. 26: 82.

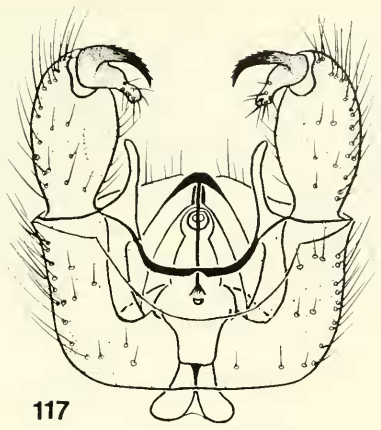
Types. Holotype, male, Madrona Camp, Siskiyou National Forest, Del Norte County, California, 1 August 1946, C. P. Alexander. Allotype, Little Phillips Creek, Blue Mountains, Umatilla County, Oregon, 2850 feet, 2 July 1948, C. P. Alexander. Paratypes, three males, same locality and date as allotype; eight males and five females from Langdon Lake, Blue Mountains, Umatilla County, Oregon, 4995 feet, 17 August 1948, C. P. Alexander. All types are in the collection of C. P. Alexander, NMNH. The holotype and three male paratypes are mounted on microscope slides.

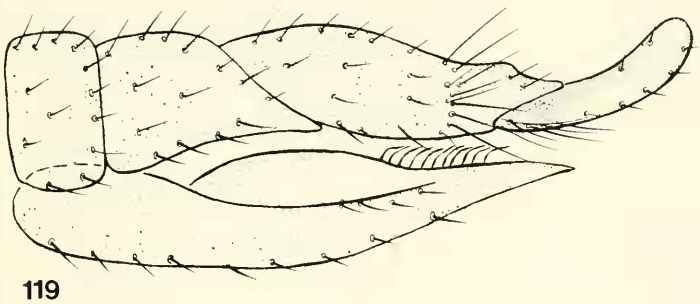
Taxonomic Characteristics. Basic coloration ochraceous. Male body length 8-10 mm, wing 9-10 mm. Female body length 10-11 mm, wing 10.5-11 mm. *Head* gray, with one row of brown bristles around each eye. Rostrum brown, palpi dark brown. Antennae with yellow scape and pedicel, flagellomeres dark brown. Verticils short, about same length as their respective flagellomeres. *Thorax* ochraceous, with light gray pruinosity on pleura. Prescutum brown without longitudinal stripe. Pseudosutural foveae indistinct. Wings with brownish tinge, highly iridescent under light at certain angles, costal fringe short and dense. Legs with coxae yellow, pruinose, apical four tarsomeres brown, remainder of legs yellow. *Abdomen* brownish yellow. In male, segments seven and eight forming dark subterminal ring. Male hypopygium (Fig. 117) yellow. Dorsal dististyle slender and evenly curved to apical spine, outer curvature denticulate on apical two-thirds. Ventral dististyle broad at base, abruptly constricted at mid-length, and with obtuse apex. Male genitalia (Fig. 118) with vesica rounded posteriorly and narrowed anteriorly. Lateral process slender, reaching to about mid-length of basistyle. Lateral apodeme expanded equally on upper and lower parts. Anterior apodemes fused medially for nearly their full length, producing a single structure about two-thirds length of vesica, narrow at base and slightly notched anteriorly. Ventral apodeme small, keel-like. Aedeagus short, bent slightly ventrad. Aedeagal process with flat plate-like upper part, dark along rounded posterior margin, connected posteriorly to rod-like lower part, hanging downward behind aedeagus. Female genitalia (Fig. 119) of *melampygia* form. Cerci shorter than tenth segment, broad, with base slightly extended laterad. Long setae near posterior end of tenth tergum and basal margins. Hypovalves extending to slightly over one-third length of cerci. Eleven setae on inner dorsal edge of each hypovalve. Postero-ventral aspect of external reproductive structure shows aperture of bursa copulatrix wider at level of membrane and narrowed anterodorsally, with receptacle for aedeagal process situated beneath it (Fig. 120).

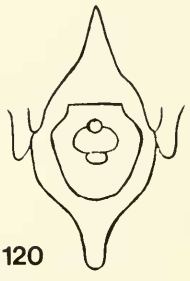
Comparative Notes. D. stenophallus resembles *occitentalis* in body coloration. Males of these two species may be readily distinguished by the aedeagal process; the former has a distinctly rod-like lower part of the process hanging behind the aedeagus, such a process is absent in the latter. In genitalic structure, *D. stenophallus* closely resembles *nigrogenualis,* particularly in having this rod-like structure, but the larger body size and dark brown coloration of the latter species make these two readily distinguishable on sight. Alexander (1967) illustrated the male hypopygium of this species from the ventral aspect of a specimen mounted on a microscope slide; therefore, the rod-like lower part of the aedeagal process (phallosome, Alexander 1967) appears curved upward in the figure.

Geographic and Seasonal Distribution. D. stenophallus is known from the Coast Ranges of southwestern British Columbia to the Coast Ranges of California, and from the Cascade Ranges to the Sierra Nevada (Map 15). *D. stenophallus* is a late summer species, as indicated by the collection data.

Summary of distribution: British Columbia - Vancouver Island, 25 August. California - Del Norte Co., 22 June, 1 August; El Dorado Co., 30 June; Humboldt Co., 7 August; Mono Co., 13 August; San Mateo Co., 8 August; Santa Cruz Co., 31 August; Shasta Co., 13 August; Siskiyou Co., 1 August. Oregon - Curry Co., 9 August; Lane Co., 15 August; Umatilla Co., 2 July, 17 August; Yamhill Co., 13-20 August. Washington - Grays Harbor Co., 20 August.







FIGURES 117-120. *Dicranoptycha (D.) stenophallus*. 117, male hypopygium, dorsal aspect. 118, left laterl aspect with external skeleton removed. 119, female hypopygium, left lateral aspect. 120, posteroventral aspect.

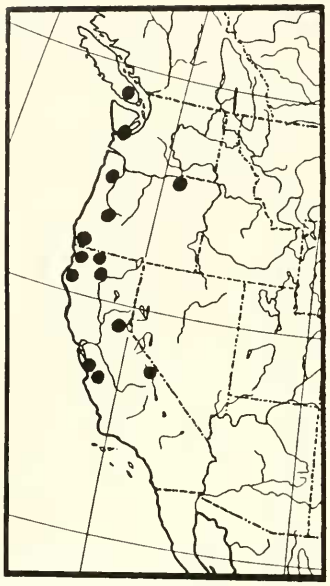
THE *LINSDALEI* GROUP

Dicranoptycha (Dicranoptycha) linsdalei Alexander

Dicranoptycha linsdalei Alexander, 1966, Trans. Amer. Entomol. Soc., 92: 110.

TYPES. Holotype, male, Hastings Natural History Reservation, Monterey County, California, 17 July 1948, J. Linsdale. Allotype, same data as holotype. Paratypes, 20 males and 18 females from type locality dated between 9 July and 20 July 1948. The holotype, allotype, five male and seven female paratypes are in CIS. Ten male and eight female paratypes are in CAS. Three male and two female paratypes are in the collection of C. P. Alexander, NMNH. Two males and one female are in the SEM. This list may not include all the paratypes that were designated originally; Alexander mentioned in his original description "paratypes widely distributed in various collections."

TAXONOMIC CHARACTERISTICS. General coloration reddish brown. Male body length 5-5.5 mm, wing 5.5 mm. Female body 5.5-6 mm, wing 6 mm. *Head* brownish gray, with one row of brown bristles around each eye. Rostrum brown, palpi black. Antennae brown throughout. Verticils about same length as their respective flagellomeres. *Thorax* reddish brown with gray pruinosity on all surfaces. Prescutum without longitudinal stripe. Pseudosutural foveae brown. Wings with yellowish tinge, costal fringe short and dense, vein 2A without setae. Legs with coxae brownish yellow, slightly pruinose basally, femora, tibiae and basitarsi yellow, with four outer tarsomeres brown. *Abdomen* with brownish yellow terga and yellow sterna. In male, segment seven dark brown, forming subterminal ring. Male hypopygium (Fig. 121) brownish yellow, dorsal dististyle denticulate on outer two-thirds of outer curvature. Ventral dististyle slightly larger, broad at base narrowed to evenly rounded tip. Male genitalia (Fig. 122) with vesica small on the dorsal aspect, with a



MAP 15. Known distribution of *Dicranoptycha stenophallus.*

large ventral part. Lateral process short, extending to about one-third length of basistyle. Lateral apodeme broad in lower part. Anterior apodemes fused along median line forming, single structure, larger than vesica. Ventral apodeme large, keel-like. Aedeagus small, inconspicuous. Aedeagal process with wide flat base and small rod-like structure posteriorly bent ventrad behind aedeagus. Female genitalia (Fig. 123) with very short cerci, about one-third length of tenth segment. Cerci widest near mid-length, with subacute tip. Long setae near posterior end of tenth segment. Hypovalve extending to slightly before base of cercus with long setae at base and along outer ventral surface. No setae on inner dorsal edges of hypovalves, hypovalve with blunt posterior end. Postero-ventral aspect of external reproductive structure as in Fig. 124.

COMPARATIVE NOTES. D. linsdalei is the smallest representative of the genus in North America. The other two small species, *D. laevis* in the West and *minima* in the East, can be separated from *linsdalei;* by having smooth dorsal dististyles, which are denticulate in *linsdalei.* Females of this species can be easily recognized by their small cerci.

GEOGRAPHIC AND SEASONAL DISTRIBUTION. D. linsdalei is so far known from only three localities in California (May 14). The type locality, in Monterey County, and the other two, Santa Barbara County and Ventura County, suggest a distribution confined to the Coast Ranges of central California. The collection dates indicate it is a late spring to early summer species.

Summary of distribution: California - Monterey Co., 5 June to 19 July; Santa Barbara Co., 7 July; Ventura Co., 10 July.

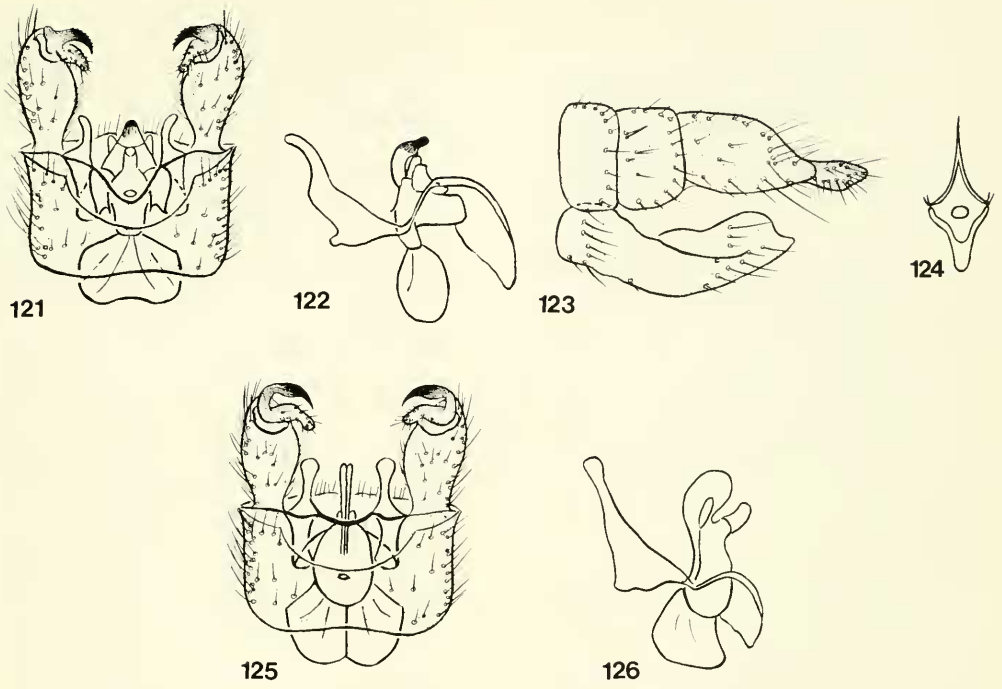
THE UNGROUPED SPECIES

Dicranoptycha (Dicranoptycha) laevis Alexander

Dicranoptycha laevis Alexander, 1947, Bull. Brooklyn Entomol. Soc. 42: 131.

TYPES. Holotype, male, Palomar Mountain, altitude 4700 feet, San Diego County, California, 12 July 1946, C. P. Alexander. Allotype, and three male paratypes same data as holotype. The holotype, allotype, and paratypes are in the collection of C. P. Alexander, NMNH. The allotype could not be located at the time I examined the type series.

TAXONOMIC CHARACTERISTICS. General coloration light brown. Male body length 6-6.5 mm, wing 6.5 mm. Female body length 6.5-7 mm, wing 7 mm. *Head* ash gray with one row of brown bristles around each eye. Rostrum light brown, palpi dark brown. Antennal scape dark brown, pedicel brownish yellow, flagellomeres brown. Verticils about one and a half times length of their respective flagellomeres. *Thorax* light brown. Prescutum darker with two obscure brown stripes. Pseudosutural foveae indistinct. Wings with grayish tinge, costal fringe short, vein 2A without setae. Legs with coxae and trochanters yellow, remainder of legs and proximal four tarsomeres light brown, apical tarsomeres brown. *Abdomen* grayish brown. Male with darkened subterminal ring on seventh segment. Male hypopygium (Fig. 125) with dorsal dististyle narrowed at base, expanded at mid-length, then narrowed into terminal spine. Ventral dististyle slightly longer than dorsal one, with rounded tip. Male genitalia (Fig. 126) with rounded vesica. Lateral process extending to about mid-length of basistyle. Lateral apodeme broad in upper part. Wide anterior apodemes broadly attached to vesica at base, fused medially except for slight notch at anterior margin. Ventral apodeme keel-like, well developed. Aedeagus inconspicuous in both dorsal and lateral aspects.



Figures 121-124. *Dicranoptycha (D.) linsdalei.* 121, male hypopygium, dorsal aspect. 122, left lateral aspect with external yskeleton removed. 123, female hypopygium, left lateral aspect. 124, posteroventral aspect.

Figures 125-126. *Dicranoptycha (D.) laevis.* 125, male hypopygium, dorsal aspect. 126, left lateral aspect with external skeleton removed.

Aedeagal process with two closely appressed blades, each compressed, rounded posteriorly, downwardly recurved to fuse with dorsum of aedeagus. Since female specimens of this species could not be obtained, details of the female genitalic structures are omitted.

Comparative Notes. The male of *D. laevis* is readily distinguished by its unique aedeagal process, which consists of two flattened plates that lie side by side. The smooth dorsal dististyle separates this species from the similar *D. linsdalei,* which has denticulate dorsal dististyles. Although females of this species are unknown to me, they will probably closely resemble those of *D. linsdalei,* to judge from the similarity of the males.

Geographic and Seasonal Distribution. *D. laevis* is so far known only from the type locality on Palomar Mountain, San Diego County, California (Map 14). The type series was collected in mid July.

Discussion

Species Delimitation. All species of *Dicranoptycha* exhibit moderate variation in size and color, but I do not consider these variations to have taxonomic significance in the genus. Byers (1961: 704) pointed out that size variation among flies of the same sex may result from variation in larval nutrition. Color variation may be correlated with geographic distribution, or in specimens from one locality it may result from differences in age. Most species of *Dicranoptycha* are morphologically well defined; interspecific variation in the genitalia is usually distinct, and species can to some extent be recognized by genitalial characters alone. However, in cases where the similarity of genitalia precludes their use in species recognition, other factors such as geographical distribution, were taken into account. *D. sobrina* and *tennessa,* for example, are sympatric over a large

area; they are considered full species in spite of close morphological resemblance. *D. nigripes* and *tigrina,* although similar, are morphologically distinct and allopatric. Because there is no indication of intergrades between them and their zone of contact (if any exists) is unclear, they are treated as full species.

SYSTEMATIC RELATIONSHIPS. Of the six genera within the current limits of the tribe Limoniini (Alexander, 1942), *Dicranoptycha* is morphologically and biologically more distinct from the other five than they are among themselves. On the basis of characters of the immature stages, *Dicranoptycha* has been considered as having closest affinities with *Antocha* and *Rhamphidia* by Alexander (1919b), and with Atarba by Rogers (1927). Of these, only the first is in the Limoniini. Unlike most genera in the tribe Limoniini which spend their immature stages in semi-aquatic situations, the larvae of *Dicranoptycha* live in the upper layer of soil under leaf mold. The origin of the shift to this much drier larval habitat forms an interesting subject for speculation.

It has been assumed that crane flies as a group arose from ancestors whose larvae, though terrestrial, lived in damp moss. It is believed that they evolved from this semi-aquatic form to either an aquatic (*Antocha*) or terrestrial form. The wholly terrestrial habitat of *Dicranoptycha* is probably a specialization. Presumably its larvae successfully invaded the terrestrial habitat early during the evolution of the genus and thereafter *Dicranoptycha* has become increasingly terrestrial. The only other woodland tipulid genus in which the early stages are spent in relatively dry soil is *Cladura* of the tribe Eriopterini.

Several unique characters found in the larvae of *Dicranoptycha* probably are adaptations for terrestrial life. The larvae have apparently functional spiracles on abdominal segments 1-7, which are unknown in other crane flies. The body of the larva is probably covered by a secretion, protecting it from direct contact with earth particles. And the mature larva constructs an earthen pupal cell that protects it from dehydration.

PHYLOGENY AND ZOOGEOGRAPHY. Although the world-wide phylogeny of the genus *Dicranoptycha* is beyond the scope of the present study, a few tentative points can be presented on phylogenetic relationships among North America *Dicranoptycha.*

Two characters found on females were used to delimit species groups. The first is the cerci, their shapes and their lengths relative to the length of the tenth segment. The other character is the number of setae on the tenth abdominal tergum. The resulting *germana, melampygia,* and *linsdalei* species groups have both morphological and geographical bases.

The *germana* group consists of all fifteen eastern species. Females of this group have long, slender cerci and about a dozen setae near the posterior end of the tenth tergum. I consider this form of cerci primitive because it is the most common and is widely shared by crane flies of other genera (although its being common does not necessarily mean it is primitive). The *melampygia* group consists of six of the seven western species. Females of this group have broad, spatulate cerci, generally shorter than the tenth tergum, and more than a score of long setae near the posterior end of the tenth tergum and along the slightly flared cercal bases. I consider this apomorphic; it resembles that of females of the Palearctic subgenus *Ulugbekia.* The *linsdalei* group contains only *D. linsdalei* from the west coast. The female has short cerci, fused in their basal halves, and has about a dozen setae near the posterior end of the tenth tergum. I consider this also as a derived form, compared to the *germana* group. Probably all three groups differentiated and evolved in the Old World before they invaded North America, as discussed in the following section.

The widespread subgenus *Dicranoptycha* s.str. is represented by 23 species in North America, 22 in Madagascar, 17 in Asia, eight in Africa, five in Europe, three in Central America and one in India. There seem to be two species-rich centers for the genus *Dicranoptycha,* one in Madagascar, the other in the United States. Because of the abundance and diversity of *Dicranoptycha* in the Holarctic and Ethiopian re-

gions, and its complete absence in South America and Australia, it seems likely that *Dicranoptycha* arose somewhere in the Old World. Probably from Eurasia, one branch of the genus invaded Africa, and speciated extensively in Madagascar; another spread through southern Asia. A third branch, or probably three branches, migrated across the Bering land bridge into North America. The discovery of *D. electrina* Alexander (1931b) in the late Eocene Baltic Amber is of exceptional interest, for it is nearly identical to some modern forms. An existing species that has a distinct wing pattern similar to that of *D. electrina* is *D. keiserae* from Madagascar. This fossil record also shows that *Dicranoptycha* has been differentiated and separated from the rest of the Limoniini since the early Tertiary Period.

Two geographic groups of species of *Dicranoptycha* can be defined in North America. The eastern *germana* group occurs mainly in the eastern forest region and as far west as the mid-western plains states. This group shows a decline in numbers of species from Virginia to Kansas and from Georgia to Canada. Among this group, *Dicranoptycha germana* has the most northern distribution, the northern limit of which appears to be in southern Canada. *D. sobrina* and *winnemana* have widespread distributions in the eastern states, reaching the plains states to the west and extending southward into central Florida. *D. elsa, septemtrionis* and *tigrina* range from the northern Appalachians westward to Kansas. *D. minima* and *pallida* are restricted to the mid-western plains states. The remaining species of this group have an eastern-southern distributional pattern, especially in the lower valleys and foothills of the Appalachians. The western geographic group, which includes both the *melampygia* and *linsdalei* species groups, is found from the Rocky Mountains to the Pacific Coast. The *melampygia* group occupies mainly the Coast Ranges and west side of the Sierra Nevada, with its center in western California. *D. quadrivittata* is the only species of this group that has an inland distribution; it is widespread along the Rocky Mountains and into the Uinta Mountains, the Colorado Plateau, and the Pacific Northwest. The *linsdalei* group, containing *D. linsdalei* and probably *laevis,* is known only from central and southern California.

That at least two, possibly four, independent invasions from Eurasia have occurred is suggested by the present *Dicranoptycha* fauna in North America. The *germana* group, structurally the most primitive, probably entered North America earlier than the *melampygia- linsdalei* or western group. This conclusion is based on the fact that the *germana* group has numerous allies in the Old World, and on the primitive or unspecialized structure of the female cerci. The ancestors of the germana group probably reached America in the Bering Strait region during the late Tertiary, when that region had a climate much warmer than it is now. Given the Eocene fossil in Europe, another possibility is that the *germana* group came across the North Atlantic when that ocean was much narrower than it now is. The group also probably ranged more widely than it does now. Pleistocene climate must have played an important role in their present distribution. The *germana* group may have taken refuge in the southern Appalachian Mountains during the last continental glaciation, with most of them migrating northward and westward after the ice retreated.

The western or *melampygia* group probably entered North America at a later date. This group is related to a similar palearctic group found in Japan, Korea and northern China. Morphologically it is most like the subgenus *Ulugbekia,* which probably evolved in Central Asia. The recent arrival of the *melampygia* group in North America is also indicated by the smaller number of species. The arrival of the *melampygia* group in North American probably resulted in the exclusion of the *germana* group from a previous western part of its range.

The structure of the female cerci of *D. linsdalei* is similar to that of several species endemic to Madagascar, suggesting that *D. linsdalei* or some ancestor of it entered North American before the *melampygia* group and is now relictual in North America. Like the *germana* group, it may have been excluded from a wider western range by the *melampygia* group. On the other

hand, it may have a North American origin, the similarity between it and the species in Madagascar being due to parallelism or convergence.

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